

Chapter 16

Predation and Muskrat Populations

IN THIS CHAPTER, I shall try to avoid unnecessary duplication of subject matter and discussions already published (see especially Errington, 1943, 1945, 1946, 1954b, 1956; Errington, Hamerstrom, and Hamerstrom, 1940; Errington and Scott, 1945). I shall here consider what, if any, are the population effects of predation upon muskrat populations. In my view, population effects of predation cannot be arrived at by merely counting the numbers of prey animals killed. Unless a prey population is reduced by predation below the levels that would evidently be reached or maintained in the absence of predation, I do not consider that the predation has population effects on the prey.]

Conventional ideas as to population effects of predation are frequently erroneous because of unwarranted assumptions. A standard thought-pattern is that if a predator kills a prey animal, the prey population must then be lower by one animal than it would have been had the predation not occurred. This would seem an obvious conclusion, but a great many natural relationships do not work out in ways that are always obvious or predictable.

Any conclusions as to the population effects of predation require critical appraisals of the factors conditioning predation, understanding of the circumstances promoting capture of prey by predators, detailed information on just what individuals of prey populations are most vulnerable to predation, and most important, long-term data on basic patterns of the prey populations living in definite areas hunted over by predatory faunas of varying densities, habits, and prowess.

HAZARDS OF USING DATA TABULATIONS IN APPRAISING POPULATION EFFECTS OF PREDATION UPON MUSKRATS

I do not mean to imply that tabulated data on muskrat populations cannot be used advantageously. Accurate and voluminous data on reproductive and mortality rates may indeed be extremely useful — provided that no greater population significance be ascribed to them than they have, that no undue concreteness be assumed for values that keep changing in reference to each other. Tabulated data may not, in themselves, insure the proper appraisal of the conditioning effects of values upon the *meaning* of other values.

There may be, for example, little real definiteness in a figure on reproductive potential or number of young produced by a muskrat female or a population sample. Extremes of underpopulation and of overpopulation, alike, may be manifested by decided irregularities in the reproductive performances of an area's muskrats. With males scarce or poorly distributed, inefficiencies in mating may result in many females conceiving only once or remaining unbred during a breeding season. With disturbances and complications of living accentuated by top-heavy densities, breeding may terminate several weeks or even two or three months ahead of the normal seasonal schedule. Or, populations of females either living in somewhat (not grossly) underpopulated habitat, or those losing heavily of their early-born young, may continue breeding much later in the season than those having good success in rearing their early-born young — even conceiving twice as many litters during the breeding season as their counterparts living under acute population tensions.

The latter phenomena emphasize the linkages between reproduction and mortality that can introduce error into calculations from tabulated data. Mortality may not have anything even suggesting a net depressive role in those cases where it serves to *stimulate* reproduction, more young being born simply because more die. This sort of compensation occurs widely and influentially among mammals and birds. Whether appraisals relate to a litter of young muskrats killed by a mink or dead of disease, or to the loss through floods of half of the young born to a whole population of muskrats, the possibility of compensatory reproduction should never be overlooked.

Mortality data may be tabulated on the bases of about anything from local investigations to continental averages. If we try to consider separately the various categories of muskrat mortality, we find ourselves confronted by values that, when expressed numerically, operate more along a sliding scale than after the manner of grade-school arithmetic. They may or may not interact predictably with each other. A value assigned to a mortality factor that merely substitutes for another — a frequent occurrence — is not the same as one that exerts a *bona fide* depressive influence on the population.

What, specifically, would be justifiable grounds for rating mink predation numerically? Mink predation has in the north central

studies accounted for more muskrats than predation by all other native predators together, yet it appeared but to have taken the place of losses from other agencies that, in the absence of minks, probably would have done about an equal amount of eliminating. Suppose that it were demonstrable — and under some conditions it might be — that mink predation increased (or its lack decreased) the total mortality suffered by a muskrat population, we can still find ourselves wondering how to weigh compensatory reproduction in the situation.

Of further bearing upon the matter of how seriously mortality figures, *per se*, should be taken are data on predation by canids. Although the numbers of muskrats killed by members of the dog family added up barely to a modest fraction compared with the number killed by minks, canid predation could have greater net effect on muskrat populations exposed to it. The distinction here is that enterprising, adaptable, and occasionally selective canids tend to be more capable of tactics permitting them to cut into populations that otherwise would not be vulnerable to wild enemies. Still, canid predation does not invariably fall in a class apart from general predation. The ordinary red fox, for example, may reveal little more originality in its day-to-day hunting than may the ordinary mink — or the ordinary cat, the ordinary horned owl, or the ordinary higher vertebrate of any species responding mainly to the chance availability of whatever it may recognize as food.

Man can be by far the most efficient of predators upon muskrats, but the population effect of even his predation may not be satisfactorily reckoned merely in terms of the numbers of animals he kills. Let us suppose that he depopulates hundreds of acres of excellent muskrat marsh in a couple of weeks' time, killing hundreds or even thousands of muskrats in so doing. How much of a biological impact would this represent? In the event of the human exploitation taking place in the autumn and leaving the best part of the marsh muskrat-vacant for many months, the mortality could be largely non-compensatory for that period. Perhaps because of the continued severity of human exploitation, the marsh might remain underpopulated, or virtually uninhabited by muskrats for years. That would have population significance. On the other hand, the depressive influence of brief though sweepingly lethal exploitation may later be more or less nullified if the depopulated tract functions as a refuge for otherwise insecure or doomed population overflows from surrounding areas.

GENERALIZATIONS AS TO PREDATION BY MINKS UPON IOWA MUSKRAT POPULATIONS

The mink has been both the outstanding nonhuman predatory enemy of the muskrat on the Iowa study areas and one studied with special care throughout the investigations. For consideration of the more technical aspects of the Iowa findings on mink-muskrat re-

lationshps, the reader may be referred to Errington (1943, 1954b).

From the latter publication the following conclusions are quoted as to categories of mink predation upon muskrats:

(a) Adult muskrats having regular home ranges on Iowa areas during the breeding months were practically safe from mink predation as long as their habitats remained in good condition. However, when put to overwhelming disadvantage, as through drought exposure, these same muskrats *could* suffer severe mink predation, to the extent of local annihilation in extreme cases.

(b) For adult muskrats that did *not* enjoy the normal security of *bona fide* residents during the breeding months, severity of mink predation was mostly a matter of the larger minks encountering land-active muskrats that were neither able to defend themselves nor to escape. Habitual transients of late spring, the surplus individuals that are attacked and injured by defenders of established territories and driven into the poorer grades of environment, had a tendency to congregate along the edges of marshes and lakes, directly in the lines of travel of minks.

(c) Mink predation upon young muskrats during the breeding months could be heavy whenever circumstances made large numbers vulnerable to predation. The main factor other than drought exposure to promote predation losses was overpopulation of habitats by the muskrats themselves. Minks preyed upon overproduced young muskrats particularly when the latter were forced into hazardous ways of life in consequence of attacks of other muskrats, as when forced ashore from the crowded wetter parts of marshes. Infection by a fungus skin disease (*Trichophyton mentagrophytes*) was another factor predisposing victims to mink predation. Young muskrats of well-situated populations ordinarily were not subject to much mink predation; many substantial muskrat populations having physical and psychological odds in their favor lost few or no young to minks during entire breeding seasons, the presence of even high densities of minks in their midst notwithstanding.

(d) Mink predation upon muskrats during the post-breeding months of late summer and fall tended to be negligible unless droughts, storms, etc., brought about crises, or large numbers of muskrats started wandering cross-country or invading habitats already occupied to capacity by other muskrats. Although these may be among the drier months of the year, an abundance of food combined with diminished breeding-season tensions often meant very favorable living for the muskrats. Furthermore, with most of the natural "shaking down" of population surpluses having already taken place by late summer, survivors had rather good prospects for continuing to survive for a time.

(e) Early-winter mink predation upon muskrats tended to be light and sporadic and centered upon the homeless, the restless, and the drought-exposed.

(f) From mid-winter through early spring, any sinking of frost lines that sealed off the food supply of muskrats in the shallower habitats and made the muskrats increasingly subject to general winter mortality also made them increasingly subject to mink predation. When muskrats frequently or regularly came out on the surface of the ice or snow to seek food in cold weather, some minks could kill them in large numbers. Late winter mink predation was often centered upon muskrats becoming restless or forced out of secure wintering quarters with the approach of the muskrat breeding season. The special targets for this predation were the individual muskrats that kept coming out on the ice during thaws, weeks before the beginning of the real spring dispersal. Severe predation upon these vulnerable individuals was followed in well-studied cases by notable absences of battered, ha-

bitual transients in late spring, and it would appear to have been the same individuals — social misfits? — that behaved in these ways, whether long before the ice broke up or long afterward.

The fundamental role of intraspecific intolerance in limiting muskrat populations was apparent by the end of the first decade of field work. Herein lay the big rigidities in the population behavior of the muskrat, those dependent upon the muskrat's own psychological make-up. On the whole, annual increases and upper levels of maintenance of muskrat populations conformed to mathematical patterns set by the species itself in relation to the supporting capacity of its environment.

Conformation to these self-limiting patterns nevertheless implied much resilience in rates of gain and loss, much natural substituting and compensating especially in the loss rates. Higher rates of loss from one agency of mortality had ways of being offset, partly or completely, by lower rates of loss from other agencies, with the totality of the seasonal or annual losses being more or less predetermined by how much a population consisted of wastage animals. With that part of a population in excess of the secure level for a given area being doomed to die, the exact fate of wastage animals made scant difference biologically.

When losses from mink predation were considered from this perspective, the severest observed had doubtful net effect on the muskrat populations of the Iowa areas as long as the habitats remained in good condition for the muskrats. During the breeding season of the muskrats, which was typically the period of severest nonhuman predation, nearly all that the minks ever were able to do as muskrat predators was to prey upon some of the more expendable parts of the populations.

In analysis, more than 70 per cent of the closely studied feeding by minks upon muskrat flesh appeared to represent scavenging, mostly upon victims of the hemorrhagic disease.

Of the feeding that represented proven or highly probable predation, about half involved victims "that had been vulnerable to mink predation chiefly for reasons of their troubles with other muskrats." About a third of the predation victims were "young muskrats caught under varying conditions of physical disadvantage, at ages at which they could have realized only a small degree of the inherent abilities of grown muskrats to take care of themselves." Most of the other victims were adults or subadults killed during acute drought or freeze-out crises.

GENERALIZATIONS AS TO PREDATION BY MISCELLANEOUS PREDATORS UPON IOWA MUSKRAT POPULATIONS

Other than minks, the nonhuman predators that have been studied with more or less intensiveness on the Iowa study areas included great horned owls, red foxes, domestic dogs, and raccoons. In addition, data were obtained from certain marshes that supported thousands of snapping turtles at times when the muskrat populations were well demonstrating their ability to increase and maintain high densities according to patterns that bore no relation to abundance or scarcity of the turtles.

Horned owl predation on the muskrats of the study areas could be negligible, even when the owls were living in the midst of great

abundances of muskrats. Formidable predators that the horned owls were, they behaved in an unimaginative manner, and their food habits were mostly determined by relative availability of prey within their hunting ranges (Errington, Hamerstrom, and Hamerstrom, 1940). The principal recorded instances of owl predation upon muskrats were of the owls responding to parts of muskrat populations made vulnerable through environmental deficiencies or evictions. Ordinarily, the presence or absence of horned owls made no perceptible difference in the fortunes of the local muskrats.

Only on drying Wall Lake in 1940 were red foxes known to have preyed heavily on muskrats, and this represented a most special case of concerted effort on the part of the foxes (Errington and Scott, 1945). The other fox predation upon muskrats was a little here and there in response to drought exposures or to muskrats coming out on ice or traveling overland.

Several examples of rather severe local "sport-killing" of muskrats by domestic dogs were noted, mostly at Goose and Little Wall lakes. These dogs often showed persistence and ingenuity in their muskrat hunting, and they seemed, on occasion, to have killed muskrats that probably would have been secure from practically all other non-human predators on the areas. Nevertheless, this sort of killing occurred on too much of a restricted scale and too infrequently to have had any more than trifling population effect. In some cases, depredations of dogs upon Iowa muskrats were a fair equivalent of those noted for coyotes in western United States.

I feel that raccoon predation upon young muskrats is as little understood as any type of predator-muskrat relationship worked with on the Iowa study areas. The raccoon depredations upon nestling muskrats at Wall Lake in 1953 may be compared, up to a point, with those reported from Atlantic Coast marshes (Harris, 1952; Wilson, 1953); but the fact that the Wall Lake raccoons confined their nest raiding to shallow water zones in disease foci is hard to explain. Granted that dying of muskrats from disease may have been what started the raccoons digging into lodges and then raiding the nests in certain tracts, why did not the raccoons raid muskrat nests in similarly accessible but disease-free shallows once they acquired the nest-raiding habit in the disease foci?

Other nonhuman predators upon Iowa muskrats include practically anything that, under conditions favoring predation, is capable of killing prey larger than a mouse. Even meadow mice may prey upon helpless young muskrats in nests, and it is not too exceptional to find newly weaned young muskrats preying upon young muskrats of the more helpless sizes.

CHIEFLY CONCERNING SOME DISTINCTIONS

In contrast with situations often found in the Far North or in desert regions where predatory vertebrates may have difficulty finding much to eat, agricultural Iowa is ordinarily rich in food for minks,

foxes, raccoons, birds of prey, and almost anything predatory that would be likely to prey upon muskrats. Although muskrats may be preyed upon by these predators, I do not know of a single instance of predators actually being forced by desperation to prey upon muskrats — though sometimes the predation was patently a result of predatory choice as well as in response to ready availability of the muskrats as prey. The mere fact that muskrats might serve as staple prey for some predators at some times does not necessarily imply that the muskrats were obligatory prey, even for short intervals. It is true, as the north central trapping public has long believed, that minks tend “to follow the muskrats,” to increase as the muskrats increase, but, insofar as that reflects responsiveness to muskrats, the responsiveness is to the muskrats as den-makers for the minks more than to the muskrats as food animals.

Not only do we have the shifting of dietary trends of the predators in response to changes in relative availability of many types of prey, but the food consumption of many common predators is not by any means expressible as a definite quantity that has to be extracted somehow out of a prey population, the year around, good years and bad. Some predators, like the snapping turtles, do not even have to be very predatory in their habits and may keep themselves stuffed with submergent vegetation supplemented by invertebrates and carrion. Other species may feed heavily or lightly, and, for the minks, pronounced extremes have been shown by field data.

From Errington (1943):

At one extreme . . . a large mink ate adult-sized muskrats . . . at the rate of about two in 24 hours. This mink was gorging to the extent that its fresh excrement consisted of pale red, raw meat. More commonly . . . minks on a straight diet of muskrats in spring consumed two or three per week. . . . [At another extreme, for minks wintering on a dried-up marsh, a] consumption rate of less than one muskrat per nine days per mink on essentially a straight diet was arrived at, and there was no reason to suspect that the minks . . . were not maintaining themselves in normal health and flesh despite thorough scavenging reflected by the dirt and heavy bone contents of many fecal passages. . . . Straight-diet rates of consumption showing all intergradations between two adult-sized muskrats per day to one per nine days alone are enough to invalidate the assumptions underlying many hypothetical considerations — and even greater differences may very likely exist in the minimal nutritional requirements of minks and the amount of food they may eat when they have opportunities.

In the region of my greatest familiarity, predatory faunas have shown both remarkable stability and remarkable variation over considerable periods of years. While food is certainly important in the ecology of predator populations, and human persecution or exploitation can be influential, I should say that central Iowa populations of able “general practitioners” among predatory species — minks and horned owls, for examples — are more apt to be limited in numbers by the intolerance they show toward crowding by their own kinds.

On the Iowa study areas, the principal native predators upon muskrats, and the muskrats, themselves, would therefore both seem to have intraspecific intolerances as their ultimate population checks — though always within the frame of reference of their habitat requirements. In other words, these predators and these prey animals are as they are with some degree of independence of each other, at least as relates to one killing and the other feeding the other. And, in still other words, much happens in these relationships between predators and prey that really does not count in population dynamics under the conditions prevailing on the Iowa study areas.

Craighead and Craighead (1956, pp. 306–10) considered “that the role of predation as a population depressant has been underestimated” and that I, in particular, underestimated its importance because of having seen it replaced by other regulating forces, of which I believed intraspecific strife to be dominant. Also:

It is likewise questionable if we can say accurately, as Errington (1943) has indicated [with reference to muskrats], that a large proportion of the victims of predation are doomed anyway, regardless of the presence or absence of predators, and therefore predation is ineffective in controlling population levels. There is no question that a certain proportion of an annual population is doomed. The important thing is not that the individuals constituting that proportion are doomed, but how they die, and that by their removal nature contrives to maintain population levels in harmony with the environment. Predation is extremely effective as a force operating in conjunction with other resistance forces to bring about this harmony. Numerous cases in which the forces of predation, intraspecific self-limiting mechanisms, and habitat limitations exerting tremendous pressure have all been necessary to check an expanding population could be cited; therefore we cannot assign a basic role to any one. It seems clear, however, that the continual pressure, governed by relative densities, that is exerted by a population of predators on prey populations is a force so powerful and so accurately meshed with all of life that it cannot be dismissed as ineffective. We almost surely shall fail to see the function of predation if we approach it from the standpoint of predation on a single prey species or predation by a single predator species, but we need only to visualize an animal community with predation eliminated to grasp immediately how important this force is and how intricate and widespread its ramifications.

We have seen that the pressure exerted by a raptor population tends to be in proportion to the relative densities of the various prey species. Thus the raptorial pressure on the prey population of an extensive area tends to depress the various species more or less simultaneously toward the threshold of security. . . . Observations of predation by a single raptor species at times will show marked pressure on one or a few prey species and will at other times show little or no pressure on the same species. In evaluating such data we should keep in mind the fact that they are only part of the pertinent information. On such a basis we could, according to the partial data at our disposal, judge predation to be either nearly annihilative or ineffective. The mechanics of predation are such that no single species in a multiple prey population can under normal environmental conditions draw sufficient predation pressure to keep its population level dangerously depressed. This we should naturally expect, and this fact cannot be used as an argument against the effectiveness of predation as a controlling or regulating factor. The killing of a prey animal by a predator does not necessarily mean a lower prey population than would have existed had the act of predation not oc-

curred; but the continual killing of prey animals in a prey population means a continuous proportional loss of animals, which tends to keep the population within limits. The argument that other regulatory forces would become operative in the absence of predation or that intercompensation (Errington, 1946) would offset the forces tending to lower populations has no bearing on the role of predation as a force regulating and at times limiting populations. The same could be argued for any other limiting factor.

As a matter of fact, if predation frequently can act as a limiting factor, and if as we have shown it becomes most effective in late winter and early spring reducing the over-wintering populations (breeding stock) then we could expect to find a reproductive mechanism evolved to counterbalance it and other depressants simultaneously operative. Compensatory breeding would appear to be such a mechanism. Just as predation or intraspecific strife are responses to high density levels, so compensatory breeding is a response to low density levels. This response is exhibited when spring to fall prey population gains show an inverse ratio to spring breeding densities. It does not indicate the ineffectiveness of predation but rather the complexity of population producing and destroying mechanisms.

It should be noted that food supply, for example, is sometimes a factor limiting populations and when this factor has a strong depressing effect, predation naturally will tend to regulate prey levels only within the limits imposed by the food supply. In such cases, predation cannot be considered the limiting factor.

Although predation can be the limiting factor, we should perhaps have a truer concept of it if it were thought of not in terms of when and how it may assume this role, but rather as a regulatory force continually operating to lower prey increase in proportion to prey density and to do this before more drastic but less steadily functioning forces become effective. These other forces seldom, if ever, affect the total prey population simultaneously, but are confined to specific prey only. Disease may strike one prey, while food shortage may regulate another. In contrast, predation strikes all components of the collective prey simultaneously and continually. . . .

As a suppressive force, predation does not reduce populations to very low numbers, as do epizootics or starvation. Moreover, the number of any single prey species accounted for may be far less than the number killed by a hard winter or a wet spring. Sudden drastic reduction in numbers temporarily releases a population from the pressure of control forces, thus allowing population densities to be again increased. This creates a type of control characterized by excessive fluctuations in numbers. Where predation is dominantly operative, however, control is characterized by continuous and proportionate reduction that tends to keep population levels near a mean. The fact that predation operates as a steadily functioning force throughout the seasons and year after year, in spite of continually changing physical and biotic conditions of the environment, gives it a great advantage, in comparison with regulators that operate intermittently or only under special conditions, in harmoniously regulating animal populations with one another and with the rest of their environments.

Although my conclusions as to population effects of predation upon muskrats were what elicited the Craighead comments, their own conclusions were drawn on the basis of experience with predation not upon muskrats but upon meadow mice. To quote again from their book:

It would appear that on any area of land, animal populations tend toward stability of interrelationships and that predation in greater or less degree

plays an important role in establishing and maintaining such a state of balance.

In this chapter, I am not undertaking any general critique of the Craighead work or philosophy concerning predation. The questions involved in a broader philosophical discussion of predation are much too complex to be treated at any length in this book, devoted so largely as it must be to muskrats. The scope of the present chapter nevertheless not only permits but also requires some discussion of the Craighead criticisms of my interpretation of the Iowa muskrat data.

I do not deny that I have different interpretations of the overall meaning of the predation borne by the Iowa muskrat populations that have been so long kept under close observation. Nor can I help questioning the validity of the Craigheads judging the population effects of predation suffered by the Iowa muskrats from no better perspective than an investigation of other animals – and from population data on prey species that collectively must be less exact than the population data that I have on my long-term specialty, the muskrat of the Iowa study areas. (See also Hamerstrom's 1958 critique of the Craighead prey data.)

I really do not know how much disagreement exists between the Craigheads and me, and the disagreement may be less than it seems. They intimated in various places that superior habitat afforded superior protection even to high prey populations, that emergency conditions could precipitate severe predation upon vulnerable prey populations, and that thresholds of security could operate in ways reminiscent of many data from the muskrat areas.

The Craigheads, in the parts quoted, wrote of the "continual pressure, governed by relative densities, that is exerted by a population of predators upon prey populations," of predation "as a regulatory force continually operating to lower prey increase in proportion to prey density," of predation as striking "all components of the collective prey simultaneously and continually." "Where predation is dominantly operative . . . control is characterized by continuous and proportionate reduction that tends to keep population levels near a mean." And, "predation operates as a steadily functioning force throughout the seasons and year after year."

Whatever may be the possible validity of the Craighead objections to my reasoning concerning other aspects of predation or other predator-prey relationships, I do not see that their idea of continuous operation of the predation factor fits in with the available data from the muskrat case histories.

It was only in 1943, that "peak" year for Iowa muskrats, that I ever observed anything having even a superficial resemblance to steady month-by-month attrition. When muskrats were then to be found in poor or good habitat generally, and appearing at times almost anywhere, the predation upon them seemed most to conform

to the Craighead concepts of predation upon the meadow mice. It was then that I was seldom surprised at finding muskrats being preyed upon, wherever they were and at any time. Still, the predation suffered by those widely distributed and abundant muskrats was by no means random nor in direct proportion to their populations. Nor do I interpret the evidence I saw as indicating that the predation was a primary limiting or regulating factor. The real limiting factor I should say was the muskrats' own nature together with the limitations of the habitat available to the muskrats. The badly-situated muskrats of 1943 could not maintain themselves indefinitely in the absence of predators, and the obviously well-situated animals got along despite the presence of minks and other formidable predators. High thresholds of security were operative in 1943 as well as in years of far fewer muskrats.

In general, our closely studied Iowa populations of muskrats did not show steady attrition after the breeding season. During the breeding season, and for a few weeks after weaning, much wastage of immature animals might occur; and predation was one of the agencies of the mortality suffered by the overproduced or vulnerable young. When this biological shaking-down was over, the rest of the population might be remarkably secure from native predatory enemies for months. Moreover, this period of security from ordinary predation may be prolonged into the winter, until the social intolerances of the next breeding season or environmental crises again increased the vulnerability of certain members of the muskrat population.

Substantial or, at times, very high muskrat populations may live the year around in the presence of heavy mink or fox or raccoon or horned owl or snapping turtle populations without suffering more than trifling losses from any kind of predation. Local populations may level off and maintain themselves according to about the same patterns when predation losses are light, moderate, or heavy, whether predation occurs through the agency of one predator or many.

I doubt if I can advance any all-comprehensive formula by which the role of predation in the population dynamics of muskrats or meadow mice, of vertebrates or invertebrates, may be expressed. Never have I maintained that predation *cannot* be at some times and places a limiting factor with some prey populations. Nevertheless, the following point of view has nothing in it that seems illogical to me: *The more a prey population is basically limited by nonpredacious factors, including its own intolerances of crowding, the less it can be basically limited by predation.* To this may be added the corollary that the "less that strong territoriality or other self-limitation enters population equations, the more something else may do the limiting" (Errington, 1956).

Exact details relating to the differences between security of muskrats from, and vulnerability to, minks and other subhuman predators are rarely available. In part, security of the muskrats appears

to be a matter of predators not readily finding prospective victims; in part, to active defense by muskrats that are themselves formidable enough, singly or through concerted attack, to drive off or keep at bay enemies, including fully functional minks; probably mostly, to adeptness in utilizing escape facilities offered by familiar grounds and suitable combinations of water and shelter. The comparative safety of daily routines of individual muskrats is linked not only with environmental features, such as the position and quality of food resources with reference to dwelling quarters, but also with the psychological status of the animals.

There are two periods when thresholds of security for adult or grown muskrats may clearly be recognized from the Iowa case histories: one in the fall and the other in the spring. The fall threshold determines the number that can then be accommodated on a given area under nonemergency conditions without undue losses from non-human predation or from departures, and the population tends to reach and to level off at this threshold value. The spring threshold has a decidedly lower numerical value than the fall threshold, at a time when social tensions among muskrats reach their maxima. A third possible threshold seems to be determined by the numbers of young that adults and large young, collectively, will tolerate on an area at the height of the breeding season; it may permit much higher densities of muskrats to be reached on a given area during the breeding months than can be maintained there later in the year. I am not sure, however, that this third type represents a very definite value at any given time or place; but the values for the other two may show a fair degree of uniformity from year to year as long as environmental and psychological changes affecting muskrat populations do not become too pronounced.

OF PREDATION AND MATHEMATICAL MODELS

Much laboratory experimentation has been devoted to the mathematical expression of predator-prey relationships (Andrewartha and Birch, 1954), and there have also been a great many efforts to express these relationships mathematically on purely theoretical grounds. No one has, to my knowledge, succeeded in constructing a mathematical model that adequately reflects predation upon muskrat populations. Of the population students I know, I think that Nicholson (1954) and Cole (1954a) have come, to quote from my paper (Errington, 1956),

the closest to depicting relationships that I personally have observed in nature — particularly the mathematical expressions of thresholds of security, overflows from favorable into unfavorable habitats, and compensatory trends.

Ideally, perhaps, everything that happens should be expressible mathematically, but, in the matter of population equations, I would say that the mathematicians have some distance to go. They have an imposing array of analytic pitfalls to avoid, and some of my mathematician friends confess that they do not see how anyone is ever going to put down on paper true-to-life

mathematical expressions of the sorts of population relationships that are commonplace among higher vertebrates. But the potentialities of mathematics as an analytic tool in population studies should be far from exhausted at the present time. What I am stating here is not intended to discourage mathematicians from going ahead with any promising approaches that they might have. My purpose is only to emphasize that, to be true to life, the mathematical expression of a population equation must not assume constancies that are not constant or more randomness than exists, and that it must not fail to take into minimal account the capacities for adjustments that living species have acquired during the millions of years that they have lived their lives in their own ways.

And thus, at the end of this chapter, which deals with some of the most carefully studied phenomena in the whole field of population dynamics of the muskrat, I find my thoughts tending to be dominated by what our knowledge of predation lacks rather than by what the studies have so far accomplished.

At any rate, we still have as subjects for our attention animals that are quite disinclined to serve as prey for anything, and which, under favorable living conditions, may not need to let themselves be preyed upon by much of anything—that is, except by that distinctively special enemy, man. The muskrats themselves have nothing to prove, disprove, rationalize, or explain, and, being to some extent free agents, they do not necessarily have to do things one way if another way will suffice. Their job is living, and they work at it full time.