creative engineers, is not the type of training that can be provided by attending three classes a week—possibly in the evening hours—and working at a regular job the rest of the time. Research work is not a series of college courses; it is a way of life. And I do not believe that either a scientist or an engineer can become fully qualified for research and development work unless he has actually lived full time in the atmosphere of a graduate institution, fully immersed in some phase of its research program. It is quite possible, of course, for a man to have an industrial job during the summer months and it is also quite feasible, if commuting distances are not too great, to work at a job 10 or 15 hours a week and still carry on a normal full-time graduate program. Nevertheless, it should be recognized that every hour spent away from the campus, from the classroom, the library, or the research laboratory is something to be avoided if possible, for it detracts from the full-time devotion to the life of research—a life that must include time for reflection and study.

Therefore, I should like to urge universities to use their influence to stem the spread of so-called "cooperative programs" in which it is assumed that graduate work and training for research can be achieved in only a few hours a week spent in a university classroom, while the student is carrying on a nearly full-time job. At the same time, I would urge industry to develop methods of expanding their fellowship programs and other ways of making it possible for their employees to spend full time on their graduate work and still receive adequate stipends.

Another barrier to the expansion and improvement in quality of graduate work in engineering is, of course, the matter of teaching. First-class creative engineers, who are the only ones who can supervise first-class graduate study, are in great demand in industry at salaries that are, quite normally, at least double the salaries available in even the best paid university faculties. Here, therefore, I must repeat the suggestion I made a short time ago that a few schools of engineering in the country which already have good graduate schools be given adequate support to increase the salaries of their key people by 40 to 75 percent in order to keep and attract the top-notch engineers required for an adequate graduate program.

These then are a few of the things that should be done to improve both the quality and quantity of our engineering and scientific manpower. Much of my argument can be summed up by saying that we ought to take our capitalistic system more seriously; we ought to offer larger rewards to those doing the most important jobs. Fifty thousand dollars does not make a good engineer; but it may prevent a good one from being diverted to other pursuits.

Factors Limiting Higher Vertebrate Populations

Paul L. Errington

At times, in seeking to generalize, a student of animal populations may feel that almost anything can and does happen or that the one common propensity of animals is to live if they can and die if they must. Nevertheless, some patterns are coming to stand out in the population dynamics of many species of animals.

My own studies of such patterns have dealt with what are commonly thought of as limiting factors in mammal and bird populations, and, in this connection. I have observed that important aspects of competition and predation may be particularly misleading if certain natural relationships and adjustments are not adequately taken into consideration. The following discussions will therefore present some of my ideas of distinctions that are worth keeping in mind when one attempts to analyze effects of competition and predation on population in at least mammals and birds (*1*).

Competition and Habitat Selection

There may be circumstantial evidence seeming to link changes in distribution or abundance of animals with changed intensity of competition. Of two closely related or closely associated species, one gains as the other fades. But, is one species displacing the other or "competing it out," as through greater aggressiveness, or are both merely responding to such habitat changes as are favorable or unfavorable to one or the other?

We do know that ascendancies and declines of bobwhite quail and of certain species of grouse have accompanied different stages of human settlement in the north-central United States, and we know that, for the grouse—pinnated, sharp-tailed, ruffed, and spruce grouse—the habitats of one species grade off into habitats of the next species ecologically in line. Yet the segregation of these native gallinaceous birds into their own niches is not so complete that it rules out possibilities of tension zones where one species could well have a depressive influence on populations of another. In cases marked neither by overt antagonisms nor by destructive impacts of one species upon the other's food supply or general environment, evidences may be seen of differential mortality or of withdrawals of one species into poorer habitats. But, again, in so many cases of what *could* be significant interspecific competition, we must return to such questions as: How much may the observed phenomena be due to something else—for example, to responsiveness to habitat niches?

The distinguishing features of habitat niches for a species are often too elusive for human perception. The main criterion for judgment may be the behavior of the species, itself, considered over sufficiently long periods of time to be meaningful. Svärdson (*2*), writing of competition and habitat selection in Swedish birds, describes the establishment of wood-warbler breeding territories at the same places but by different individual male warblers each spring. Despite local differences in topography, vegetation, and light conditions, selection of the old territorial sites by newly arrived, strange birds proceeds according to pattern each year. After very intensive studies, McCabe and Blanchard (*3*) concluded that the three species of California deer mice with which they worked have

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an extreme sense of environmental specificity, which serves to keep members of each species segregated into niches.

It could be contended, I suppose, that it would be a peculiar animal that did not recognize its proper habitat when it found it, irrespective of the numerous examples that might be listed of animals pioneering into new habitats or otherwise trying to live somehow even when they find themselves outside of anything resembling a proper habitat. The gradations in suitability that habitat niches may show for their occupants may, however, lead one to ask just when enough is enough, when marginal habitability becomes submarginal or worse. Svärdson's studies of competition emphasize the tendency for strong *interspecific* competition or population pressure to cause a species to retreat to those habitats in which it is particularly adapted to maintain itself. Conversely, strong *intraspecific* pressure may force the species into a much greater variety of habitats, including those that may scarcely be defined as habitable for the species trying to live in them.

Of course, if we look for examples of animals either living in very restricted niches or showing spectacular mass increases or invasions or colonizations of new habitats, we can find them all the way down the phylogenetic scale from mammals and birds. We need only consult the vast entomological literature. Or, we can go down toward that nebulous line of demarcation between what is living and what is nonliving.

I have worked on the epizootiology of what can be an extremely contagious and deadly hemorrhagic disease of muskrats. The full etiology of this disease, in my opinion, remains undemonstrated; but, whether the available evidence suggests a viral or a bacterial agency, or a combination of them, or something else, the manifestations of the disease in our Iowa study areas are all but restricted most of the time to certain special tracts of marsh or stream. In thinking over the long-term case histories of these foci of infection, I keep comparing them with our case histories of strategic habitats for the muskrats themselves, or with strategic habitats for bobwhites, pheasants, horned owls, minks, rabbits, foxes, and other higher vertebrates, or with those kinds of strategic habitats that Uvarov (*4*) and later authors call areas of permanent occupation for grasshoppers and locusts.

When we look for further parallels between population behavior of the muskrat disease, of the muskrats, of the bobwhites, the pheasants, the grasshoppers, we may often find them if we consider overflows from strategic habitats. The muskrat disease, if it spreads from a focus of infection into an adjacent part of a marsh having a dense contiguous population of the host animals, may virtually depopulate a large tract of its muskrats in a few weeks; but, when the dying subsides and the depopulated tract begins to draw in newcomers, about the only places where we may expect renewed flaring-up of the disease will usually be at or near the old foci of infection. At the risk of minor inaccuracies, we may say that the contagion seems to withdraw into its own areas of permanent occupation—at any rate, to these places that retain sufficient infectiousness over the years to be reservoirs.

When many animals overflow their strategic habitats, it may be only into places nearby or into places perhaps not differing greatly from the strategic habitats, or it may be into strange and inhospitable places. Muskrats of overpopulated desert marshes may engage in fatal movements into the surrounding desert in ways reminiscent of the famous migrations of Scandinavian lemmings into the sea. Overflows of muskrats often may be not very dissimilar to the overflowing of certain grasshoppers and locusts from their breeding grounds, the special aspects of the latter movements notwithstanding (*5*). Pepper (*6*), in comparing thresholds of security and associated phenomena shown by our Iowa muskrats with what he had been seeing in Montana grasshoppers, brought out similarities that look very suggestive of common denominators in the population behavior of even such distantly related forms.

The main point that I would make here is that, whether a species is intrenched in the best of habitats or is trying to live where it really does not belong, whether it is highly versatile or has the most specialized of adaptations, the role of competition in its population dynamics may still be more difficult to appraise than may at first be apparent. To distinguish between cause-and-effect relationships and the merely incidental may require, for one thing, less emphasis upon what seems obvious and more emphasis upon trends indirectly suggested by long-term data.

Let us, for the time being, go on to other subject matter notable for the ease with which it may be misappraised.

Predation and Territoriality

Predation may have its superficial simplicities. It may look as simple as one animal killing and eating another animal. When the victim is dead, it is dead, and the species to which it belongs has one less living individual. From here, it is possible to make many speculations about the effects of predation on population, especially on the theme of how high the population levels of prey species would go were it not for predators preying upon them. It is frequently assumed that a predatory species exerts a limiting influence on a prey population about in proportion to the number of prey individuals it kills.

Predation, assuredly, *can* depress a prey population. Under special conditions, the impacts of a predator on its prey can be so severe that whole populations of a vulnerable prey species are wiped out. Predatory man has demonstrated this over and over again. On the other hand, the accrued evidence indicates that much predation may operate in an incidental fashion rather than as a true population depressant (*7*). The distinction to be kept in mind is that predation centering on essentially doomed surpluses or wastage parts of prey populations is in a different category from predation that cuts right into a prev population and results in the prey's reaching or maintaining a significantly lower level than it would if it did not suffer such predation.

In analyses of the population dynamics of animals, we must not ignore the role of social intolerance as a limiting factor. Social intolerance may or may not be tied up with food supply or other of the more obvious needs of a population at a given time. The more dominant types of intolerance include those that we think of as territorial, even when habitat resources may appear to be only slightly utilized by the individuals claiming possession.

Territoriality is variously defined in the literature, but the definition of a territory as any defended area is one of the most acceptable (*8*). In its manifestations, territoriality varies greatly with the species and the circumstances. It is not lacking among invertebrates and lower vertebrates, although, in those groups, its intensity may be weak, or we may have to strain a bit to apply the label of territoriality to certain intolerances. Nor are the more pronounced forms of territoriality to be perceived among all higher vertebrates. Still, the higher vertebrates include the most patently territorial groups of animals and those patently the most nearly self-limiting.

Self-limitation is about what strong territoriality adds up to in population dynamics. It allows *Lebensraum* for about so many animals of one or, sometimes, a combination of species at a given time and place. Compared with the basic role of territoriality in the population of many higher vertebrates, predation enters in as a secondary phenomenon and as one having, in more instances than are usually recognized, slight if any real depressive influence on prey populations—even when the predation may be severe in terms of numbers or proportions of the prey species killed by predators.

When a strongly territorial species fills up its habitat as much as the species will itself tolerate, and the surplus individuals cannot live anywhere else, the species may maintain its numbers with a high degree of independence of variations in kinds and numbers of predatory enemies. The muskrat in the north-central United States illustrates this sort of relationship, and we may see, for this species, that a great deal of the frequently conspicuous and severe interspecific predation does not really count (*7*).

If surplus individuals excluded from the better territorial sites can live in the less attractive places in the absence of but not in the presence of certain predatory enemies, the resulting predation may operate to some extent as a population depressant in the inferior habitats. This situation may be not uncommon when the prey species is one showing versatile behavior.

Some higher vertebrates may be sufficiently tolerant of crowding to increase up to the limits of their food supply in the absence of significant predation. North American deer are among the better known examples (*9*), but, on the basis of careful work on California deer herds (*10*), it would appear that the deer population is primarily determined by quality of habitat and that predators do little more than to remove the annual surplus. In many areas, striking increases in numbers of deer have been correlated with artificial reduction of the more efficient deer-killing predators. The deer populations have then built up to temporary levels above the carrying capacity of the land, with biological repercussions coming later, as from starvation or damage to the habitat. While territoriality exists for the deer and represents, for them, a self-limiting tendency, it does not limit enough to leave deer populations in quite the same category of independence from influence by predation that follows, for example, from the stronger self-limitation of the north-central muskrats.

It is quite to be expected that some animal species will show greater tendencies toward overpopulation, overuse of resources followed by population collapses, and, on occasion, by net depressions of population levels through predation, than do our more strictly self-limited species. The less that strong territoriality or other self-limitation enters population equations, the more something else must do the limiting.

Competition, Predation, Compensations, and Models

The quest for generalities in the population behavior of organisms has led to a substantial amount of laboratory experimentation (*11*). Oversimplifications and artificialities need not detract very much from the interest and value of these experiments as long as the experimental results are not misapplied to relationships that are far more complex. In working with field problems, we may think of the better conceived laboratory experiments with populations as suggesting rules of order that we ought to know something about before we go on to consider the interplays, interruptions, deflections, and successions that characterize free-living populations.

Based either on experimentation or on purely theoretical grounds, many efforts have been made to express population relationships mathematically. I make no pretense of being able to examine the resulting mathematical treatments with any notable competence, but I have recognized that those of Nicholson (*12*) and Cole (*13*) seem to come 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.

Elton's (*14*) essay on animal community patterns emphasizes the grouping of populations around centers, in contrast to mathematical theories that treat populations as if they are randomly interspersed over major areas. Differences in soil types, warmth, moisture, plant successions, the location of a carcass or a rotten log, the segregation into habitat niches, and so forth, may leave scant uniformity in the natural distribution of a species and thus reduce the prospects for finding true-to-life formulas that apply to the more complex situations.

Let us consider the way in which the hemorrhagic disease may kill muskrats on a marsh when the muskrats are so few in number as to be barely present and when, according to some mathematical models, we should hardly expect continued dying. In nature, we can have the *entire* local population dying and newcomers dying about as fast as they come in. The reasons for these high mortality rates at times of very low over-all population densities on the marsh are, in their gross aspects, quite plain—they chiefly reflect the fact that the deadlier foci of infection may also be among the more attractive places for muskrats on a marsh. The more that perfectly normal newcomers pick out and rehabilitate deadly burrow systems, the more die there, and the deadlier the burrow systems become over the years, until certain tracts of marsh may become all but uninhabitable for muskrats for years at a stretch. Under these circumstances, I cannot see that so very much of randomness is left in the population equations of either the hemorrhagic disease or its muskrat hosts.

Some remarkably definite patterns are shown by case histories of free-living wild populations, but it can be tricky to represent these in mathematical formulas. There can be much compensating in a population equation, or, in other words, automatic letting out and taking up of slack. Granted that many species can be sensitive to environmental changes of slight amplitude, we do have many populations maintained for long periods of time at notably uniform levels, more or less irrespective of a great many variations in breeding and mortality rates and in the weather, food supply, and other of what we consider ordinary environmental factors (*7, 15*).

The modern work with higher vertebrates perhaps illustrates as well as any how compensations operate, and, in order to remain within the philosophic bounds of personal familiarity, I shall draw my concluding examples from the results of our investigations of Iowa muskrats (*16*). We find in our data on muskrats plenty of evidence of conformity to patterns that are definite enough to be expressible by segments of sigmoid curves (*17*), but which mean balancing and counterbalancing in population equations. The classical Darwinian view of the balance of nature is misleading with reference to population dynamics of the muskrat because it is so apt to put nature's resiliences and rigidities in the wrong places.

Instead of a population equation in

which the end product varies directly and matter-of-factly and in an aboveboard manner according to variations in reproductive and mortality rates, we have end products that often look more or less predetermined. The latter may be a postbreeding population of around 400 muskrats on a 270-acre marsh, or 9000 muskrats on 1000 acres elsewhere, or some other comparatively definite number for another area. Or, when populations are well below saturation levels for an area, the annual rates of gain may conform to a sliding scale of values. When the end products of population equations show pronounced tendencies toward stability or conformation to patterns, the other parts of the equations are necessarily the parts in which adjustments occur whenever changes in reproductive or mortality rates would tend to disturb equilibria.

Although larger or smaller proportions of young muskrats may die from the attentions of predatory enemies or from weather vicissitudes or from attacks of other muskrats in one year than in another year, the population consequences of specific mortality factors seldom carry through long enough to affect appreciably the end products of our population equations. This, in particular, represents a departure from the Darwinian view. Instead of every agency of mortality each depressing the end product in proportion to the number of animals it kills, we have a lot of nullification of what we conventionally regard as limiting factors. Not only do we have natural substituting of one factor for another, but mortality may also precipitate natural population responses that tend to offset it.

Let us consider mink predation and the way it fits into our equations for muskrats insofar as this has been most intensively studied on a long-term basis (*18*). Minks and muskrats may be closely associated in North American wetlands, and the minks are enterprising and able hunters that kill and eat muskrats about wherever they can. In some regions, they kill more muskrats than all other nonhuman predators combined. But, in analysis, mink predation on muskrats of the north-central United States turns out to be virtually centered on overproduced young muskrats, upon ailing and battered individuals of all ages, and upon those generally comprising the wastage animals of a population. The victims need not be manifestly unfit. Insecurity of position can impose as deadly a handicap on an animal in normal physical condition as can the sluggishness or weakness of an animal that is physically subnormal.

Particularly worth emphasizing in appraisals of net population effects of agencies of mortality is the evidence that the broad categories of muskrats most likely to be preyed upon by predatory vertebrates—excluding man—have poor life expectancies, anyway. They are the likeliest candidates for elimination through one agency or another, whether the minks are abundant, scarce, or absent, or whether the other common muskrat predators are abundant, scarce, or absent. In the frittering away of doomed surpluses, or of parts of populations doomed because of emergencies, it seems to make so little difference in the end what the specific agencies of mortality may be that I rarely feel sure of the logical propriety of ascribing true depressive influence to any one agency. Of what demonstrable population significance is any agency of mortality as long as much the same patterns in population trends continue to show up, seemingly irrespective of whether that agency operates or not?

If the effects of an agency are severe enough—if a deadly epizootic, a hurricane, or a drouth brings about a cataclysm for the muskrats over an immense area—the mortality can be sufficient to depress a population, but there still may be compensation. One of the commonest ways by which extraordinary losses are offset naturally is by accelerated reproduction.

The reproductive activities of our Iowa muskrats have an obviously close connection with psychological changes. Adult females giving birth to their usual maxima of four litters during a breeding season are typically animals living at low-to-moderate densities in a strong environment or those losing large proportions of their early-born young. On the other hand, those subject to the damping effects of crowding past their toleration limits just quit breeding early in the season after giving birth to a litter or two. As long as relief from the inhibiting effects of overcrowding remains such a stimulus to prolonged, late-season breeding—as long as heavy mortality among the early-born young, or special success of the early-born in keeping out of the way of intolerant elders, or the chance underpopulation of habitats may result in doubling the number born per adult female—the need for allowing for compensations in our pencil-and-paper figuring would not appear to be trifling. As long as the end product of a population equation remains unchanged, with reproductive and mortality rates serving as functions of each other in the ways indicated, more reproduction means more mortality, and vice versa.

In short, throughout any true-to-life equation representing population dynamics of the muskrat, there should be compensation after compensation, although it does not follow that all of the adjustments involved must be completely compensatory. Perhaps few of them are completely compensatory, but neither does it follow, if any one agency kills half of the muskrats during the breeding and rearing months, that relief from that agency will double the number of muskrats alive after the breeding and rearing months, nor does it follow that the appearance of a new and deadly agency that kills half of the muskrats must thereby reduce the end product of a population equation by half.

Solomon (*15*), in his review paper on natural control of animal populations, refers to the compensation principle as being of general applicability. This has not only been discussed in regard to vertebrate populations (*7*), but Nicholson and H. S. Smith, the entomologists, also have been expressing similar views for many years. In the literature on population, the idea of populations' being to some extent self-controlled is therefore nothing wholly new. Still, the singular importance of considering automatic and compensatory adjustments in population dynamics is far too often neglected even in scholarly thinking, and a realistic approach in population studies calls for more attention to things that do not always work out with the inexorable precision that data tabulations might seem to imply.

References and Notes

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