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THE ROCKEFELLER INSTITUTE

FEBRUARY 1963

REVIEW



POPULATION CONTROL AMONG VERTEBRATES

BY ALEXANDER KESSLER

Field studies and experiments have shown how vertebrate populations regulate their own numbers by means other than the Malthusian restraints.

AT A TIME when the growth of the human population is fast enough to be described, with at least some justice, as an explosion, the question of what determines the size of a population of living things is naturally of more than academic interest. Inevitably, too, the question is a reminder of the doctrine, which Malthus advanced a century and a half ago, that populations of all kinds of living things will increase until they are held within bounds by the scourges of starvation, disease, and war.

The accumulation in recent years of field observations and experimental evidence on the dynamics of populations of various species suggests that there may be biological reasons for considering the Malthusian doctrine to be incomplete. Briefly, it appears that the populations of many species are integrated entities, with intrinsic and adaptive mechanisms which enable them to regulate the sizes of their populations. Such important determinants of population size are missing from Malthus's short list of demographic restraints.

A great many studies have pointed to the importance of interactions among the members of populations in the dynamics of their population growth, equilibrium, and decline. The influences of those interactions have been demonstrated for organisms

ranging in complexity from tissue culture cells and bacteria all the way to mammals, and this represents a real addition to the commonly recognized extrinsic factors that limit populations such as inadequate nutrition, an unfavorable physical environment, or the presence of inimical organisms. The nature of these interactions among individuals, and the resulting mechanisms which lead subhuman vertebrate populations to regulate their sizes, deserve careful attention and analysis not merely for their own interest, but also because "what is phylogenetically significant is apt to be physiologically fundamental." (Hartman)

Knowledge of the dynamics of populations is the product of several different disciplines, and the literature is scattered. In these circumstances a selection from this literature may be of some value.

Observation

That external factors such as bad weather, predation, and lack of food are not the all-comprehensive limitations they are generally supposed to be is apparent, for example, from observations such as those of Elton and Chitty of the fates of populations of field mice in an Oxfordshire meadow. Several nuclei of population were found to be established close to each other, and were kept simultaneously under observation. They were exposed to the same climate, preyed upon by the same numbers of larger predators, and equally infected by potential pathogens such as tuberculosis. Each population of mice had equal access to similar quantities of food.

The uniformity and "equality" of the extrinsic environment of each population did not, however, result in an identical pattern of population dynamics

for each group of mice. On the contrary, as observation showed, one population would grow, another would shrink, and a third would remain constant in size. Plainly, something other than extrinsic factors determined the size of each population. The efficacy of internal regulators of population has also been demonstrated in a variety of other wild vertebrate populations. These include muskrats in Iowa (Erington), flocks of great tits in Dutch forests (Kluyver), and Levant voles in Palestine (Bodenheimer).

Inevitably, however, it is difficult to extract unambiguous understanding from field studies of populations. Population dynamics necessarily entails multifactorial relationships, but these are most difficult to analyze for populations observed in the field. This is why the study of populations within the confines of the laboratory has led, within the last fifteen years, to a rapid expansion of knowledge about the dynamics of populations of subhuman vertebrates.

Experimental populations of fish, frogs, chickens, rodents, rabbits, and other species have been established in oversized containers, cages, entire rooms, sheds, and even in outdoor enclosures. Like all experimental techniques, these devices have made it possible to control at least some of the factors influencing the dynamics of vertebrate populations. They have also made it possible to follow the goings and comings of marked individuals and thus to evaluate the role of behavior in population dynamics.

Experiment

The variability between adjoining wild populations was quickly duplicated in the laboratory. The procedure was to use identical numbers of animals, sometimes taken from split litters, and to establish freely breeding populations in replicate experimental environments. Even though an abundant food supply may be provided, different populations will follow different patterns of growth.

In one experiment, for example, four pairs of mice were put into each of six large enclosures, and after two years the descendent populations were found to vary in number more than five-fold, from twenty-four to 130 (Southwick). The detailed census and observation of these and other populations has made it plain that the variation of their sizes is far from being a random phenomenon within a statistically

normal distribution. Rather, it appears that the variations are associated with specific behavioral and physiological traits within the populations.

The self-regulatory mechanisms of vertebrate populations have, in fact, been shown capable of modifying several biological processes at various stages in the life history of individuals. In different species the self-regulation of population has, for example, been accompanied by variations of the capacity of individuals for sexual activity; of the number of eggs and sperm produced; of the implantation of fertilized eggs, the survival of embryos and newborns, the rate of sexual maturation, the health of individuals, and the mobility of adults. A few illustrations will make this clear.

In their studies of freely growing mouse populations, Strecker and Emlen set an absolute limit on the total daily allotment of food placed in enclosures. When the populations had expanded to the point of incipient food shortage, two striking things occurred. First, there was a sharp rise in the mortality of juvenile mice, from ten to eighty-five per cent, soon followed by a striking and generalized depression of sexual activity. Eventually the members of this population ceased altogether to reproduce.

There was no rise in mortality among adults, nor any fighting, and the fat appearance of the adults indicated that self-regulation had occurred when nutrition was still adequate. The depressed sexual and reproductive functions of females from these populations were reversible, since these could promptly be mated successfully once they had been removed from the regulatory influences of their population.

Most frequently, however, the self-regulatory mechanisms of vertebrate populations appear to act differentially on the individuals of population. Thus Calhoun observed a population of Norway rats grow up from a single reproducing female in a quarter acre enclosure over a two-year period. This population clearly regulated its size as a unit, for in this large enclosure with ample food, sufficient to accommodate 5,000 rats, the population was established at 120. Within it Calhoun was able to distinguish eleven subgroups of rats, each with different numbers of males and females and different reproductive characteristics.



ents, who must provide food, warmth, protection, and the many other forms of stimulation needed for the development of proper physiology and behavior. In several experimental studies of rats, house mice, voles, and rabbits, high neonatal litter mortalities have played a prominent part in stabilizing populations.

Among fish, analogous self-regulatory mechanisms lead to fairly stereotyped and repeatable ceilings of population. In a classical experiment, one population was descended from one gravid female guppy, and a second population was initiated in an identical container by fifty guppies of varied size, male and female. After six months both populations reached the same stable complement of nine individuals. The opposing influences of variable fertility on the one hand, and infanticide and fratricide on the other, were called into play as the equilibrium populations were approached from below and above.

Similar self-regulatory processes appear also to affect expansions and declines of many wild vertebrate populations. During attempts to control wild rats in Baltimore, trappings, markings, and releases of animals revealed that one city block would have a fairly stable population of animals. Rats stayed on their own block in much the same way as if they had belonged to an experimental population and repulsed intruders from elsewhere. A population

Some subgroups had few males and many females, and these females were successful in rearing litters or were pregnant when the study ended. Other subgroups tended to have more males to each female, and the latter were less successful in reproduction. Still other subgroups consisted only of males or of males with a few females so reproductively ineffectual that they could be counted as asexual. Clearly self-regulatory mechanisms had differentiated the population into a small fraction of actively reproductive animals compared with a larger reproductively inactive population.

Among vertebrates, and especially the higher ones, the rate of survival of the newborn is one means by which the size of a population is regulated. For survival requires appropriate behavior by par-



would exhibit all the marks of self-regulation and its size would be considerably below the carrying capacities provided by garbage and harborage. In a similar vein, several studies of wild rabbit populations have indicated a generally inverse relationship between the number of rabbits in a given area and the rate of intrauterine mortality or the sizes of litters.

Among birds, Kluyver's long-term observations of great tits suggest that the annual egg output of a breeding female can vary from nine when the population density is high to fourteen when it is low. Food shortages played no part in these variations. Then there are many descriptions in the ornithological literature of the destruction of their own eggs and young by herring gulls, terns, storks, razor bills, and many other species, and these happenings were not accounted for by particular environmental conditions such as a shortage of food. These practices are analogous to the behavior which leads to litter destruction among small mammals and their prevalence suggests that they may represent adaptive traits by which the size of populations may be regulated.

Vertebrate populations are "entities that are more than statistical summations of individuals." (Emerson) They are unified by the patterns of social behavior of their members, and these exist, and can develop in individual members, only within the context of the population. Among vertebrates social behavior takes many varied forms—in activities such as mating, parental care, grooming, and the like.

Society

Dominance hierarchies and territoriality are two other patterns of social behavior found among all vertebrates; and the way in which these serve to integrate vertebrate populations appears to be fundamentally related to many of the self-regulatory mechanisms within these populations. Both patterns involve competitive interaction between individuals, and this leads in hierarchical populations to domination by a single despot or by an oligarchy of despots, or to the establishment of different gradients of dominance. Organization or integration are the products of the networks of specific relationships thus established.

Where territorialism is the unifying principle, the interaction between individuals is more obvious and rests on the competition for a limited number of unit plots within the wider territory of the population. The members who acquire land are brought into frequent contact with one another as they reaffirm the boundaries of their unit plots in direct encounters, by sounds or by other means. That this integration of populations is real and that it provides cohesion is well demonstrated by the clear-cut recognition and exclusion of outsiders from populations organized on hierarchical or territorial lines.

In both types of society successful competition confers on an individual a number of privileges such as the access to mates and to food, free movement, and membership of the group. Unsuccessful animals, on the other hand, may be denied some or all of these, but several observations have shown that there is no direct competition for the privileges themselves—mates, food, and the like. Thus the sexual behavior of low-ranking males among domestic chickens is inhibited even when the dominant male is removed from the pen, although such a subordinate male will readily mate with hens from another flock. Similarly, in his description of rat populations, Calhoun has noted several kinds of what he calls "socially castrated" rats, both male and female, distinguished by a complete lack of sexual interest.

In hierarchical societies the association of dominance and feeding was originally noticed by Schelderup-Ebbe, who observed that subordinate chickens would yield their places at the feeding-box to the dominant members of their group. Similar behavior has since been observed in populations of mice, voles, apes, and other vertebrates. The fact that social competition is frequently most intense just before the reproductive season enhances its influence on the dynamics of a population.

Another important mechanism by which social behavior is linked to population control is by means of the banishment of individuals, or their forced emigration if this is ecologically feasible. Thus it has been observed that Australian magpies excluded from the territory of their flock have simply failed to mature sexually, and "for these the stimulus of the changing seasons was not sufficient to bring the birds to sexual maturity." (Carrick, quoted by Andre-

wartha) That development, indeed, seems to require some stimulus derived from membership of the population of an established territory, for even when groups of excluded individuals gathered together, reproduction did not take place.

Outcasts may also delay in finding suitable breeding sites, and at the same time appear to be particularly vulnerable to disease, predation, and accident. Thus Carrick found that magpies excluded from the territory of the flock were especially susceptible to parasites. Errington, while carefully examining the remains of muskrats found in the intestines of their predators, noted that of 2415 muskrats recovered, sixty-five to seventy percent represented previously diseased animals or otherwise demonstrably subordinate individuals. Thus, external forces which have long been considered as restraints on populations do, indeed, operate by the elimination of individuals, but these individuals are those that are selected as surplus by the social competition of the population itself.

Though success is obviously vital, social competition rarely leads to killing of competitors. To be sure, mortal combat has been seen in experiments in which two or more strange adult males were placed in a small and confined area, but this is exceptional both in experimental populations and in nature. More frequently the subordinate individual quickly comes to recognize the status of his superiors in more subtle ways, and so withdraws. In many species aggressive behavior appears to have been displaced and competition to have taken the form of mutual displays of flight patterns, ritualized stances, and other forms of noncombative communication.

Competition

For the most part it seems that social competition is the function of the male sex, at least in the majority of vertebrate populations. The reproductive fortunes of the female depend on the status of the male by whom she is accepted. Females who are associated with subdominant males in experimental populations may fail entirely to reproduce.

Thus in both hierarchical and territorial systems, populations are divided into animals which breed and those which do not, and this in itself is one of the fundamental steps of self-regulation of numbers.

But the intensity of the social competition is also a function of the number of individuals competing. In other words, the larger the population, the more intense the competition for status or territory is likely to be, and the social tension thus generated will in turn activate regulatory mechanisms that ultimately help to determine population size.

Among the highest vertebrates (such as small mammals) attempts have been made to quantify the amount of social tension in populations.

Stress

The idea is that population density is in itself a form of stress that may act to change the activity of certain endocrine systems, such as the pituitary-adrenal and the pituitary-gonadal axes. The relationship between stress and adrenal activity seems to be affirmed by the observation that among mice the dominant individuals, which are the least stressed, have the smallest adrenal glands, and that subordinates have the largest. Thus Christian and many others have weighed the glands of whole populations, both wild and experimental, and have correlated the amount of adrenal activity with the density of the population. In general, higher population densities are associated with larger adrenals, which lends some weight to the hypothesis that social tension increases with population size and density.

Suggestive though it may be, this evidence should not be taken as proof of a universal direct relationship between population density and social stress, however. Experiments have indeed shown that there may be considerable variations of adrenal activity among populations which are identical in size. Small populations may even be characterized by a degree of adrenal hypertrophy as great as that found in much larger populations. This is to be explained by the assumption that the degree of social tension generated in a small or sparse population can at times be equal to that in a larger and more dense population. Corroboration has been provided by direct observation of distinctive behavior in mice from small populations in experiments in which the final size of replicate and freely growing populations varied through an eight-fold range.

The genetic implications of some of these integrative and self-regulatory mechanisms are consider-

able. The experimental evidence suggests that the breeding structure of a vertebrate population is established primarily on the basis of patterns of social behavior. Social hierarchies and territorial systems act directly to determine who shall and who shall not breed, and thus become forces of selection, or of social selection. Thus even among subhuman vertebrates, social behavior can be a cause of evolution, as well as one of its consequences.

Success

It is in this connection, of course, that it would be most important to understand what attributes go to the making of individuals who are successful in social competition. Unfortunately the roots of an individual's success are often not clear.

Age, size, previous experience (and especially victory in combat), being on familiar ground, and heredity have all been implicated. For example, in a population cage with centralized feeding areas, there is a high probability that a young animal will encounter older and dominant ones. Frequent losses in these encounters have been shown to have a lasting influence on a young animal's chances of rising to dominance later on. Among wild populations entirely analogous situations arise when food supplies are highly localized or where emigration is ecologically not feasible. The importance of being on familiar ground is evident in the ability of a small bird or mouse, ensconced on its own territory, to chase away much larger rivals.

The contribution of heredity to success in social competition is hinted at in some studies concerned with the relationship of aggressive competitive be-

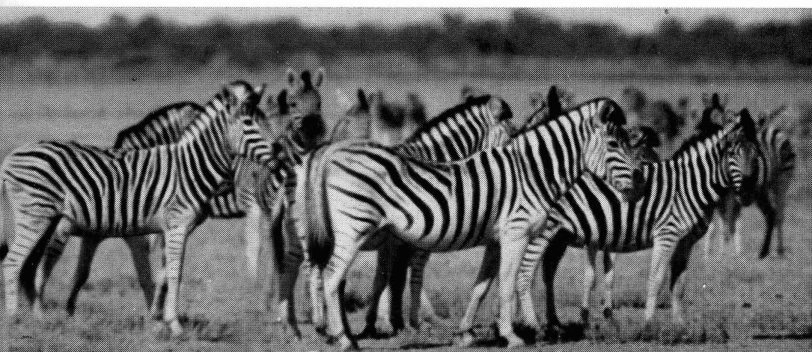
havior and dominance. For instance, game cocks tend to be dominant when matched against hybrid cocks. Terriers, an aggressive breed, tend to dominate beagles in experiments in which animals of both breeds were reared together from birth. Black, agouti, and albino C 57 mice rank in that order from most to least aggressive in artificial experimental competition. There are strains of fearless and strains of timid albino rats, and when individuals from these strains are placed together, inherited aggressiveness wins out.

So far, however, there is no evidence of the extent to which the young of dominant individuals in actual populations are themselves genetically endowed to become dominant. If, indeed, there is a genetic basis for dominance, it is likely to be complex and genetically balanced, for otherwise it would rapidly out-select itself.

There is, however, some evidence to suggest that certain genotypes simply cannot survive in any social context. Thus Calhoun established freely growing experimental populations in the usual way, but used as starting animals individual mice that had been through extensive selection for various traits, and had been reared for many generations in a restricted social environment. One strain was physiologically unstable and susceptible to seizures, tumors, and the like. The other strain was physiologically more stable. The social behavior and adjustment of the two strains were quite different, but social life, especially when the population density was high, was too full of stress for the physiologically unstable strain and its members died off rapidly.

Eventually hierarchical and territorial systems set

The sizes of game populations in Africa are normally controlled without the intervention of hunters.



*A population of
sea lions basking
in the sun in
Lower California*



the stage for what is called genetic drift. Both social patterns tend to discourage immigration and gene exchange by surrounding the population with behavioral as well as geographic boundaries; they tend often to isolate small groups and further, to provide for selective breeding within their groups. Unfortunately, too little is known about the dynamics of gene frequency in small wild groups like these, defined and delimited as they are by patterns of social behavior rather than by vague geographical limits. This fact is clearly recognized by Lewontin and Dunn who state, in connection with the distribution among populations of wild mice of a particular system of alleles related to tail structure, that "mice in the localities of capture have been referred to as populations . . . this has only a geographic but not a biological meaning."

An explanation advanced by Lewontin and Dunn to account for the occurrence of this allelic system among populations of wild mice bears an interesting relationship to the known patterns of social behavior among wild mice. The allele in question is the t allele, which is essentially lethal when homozygous, so that it should tend to be eliminated from

small populations. Though mutations from wild-type alleles to t are unknown, the t allele occurs in fairly large numbers in all wild populations of mice in which it has been sought. To account for this puzzling persistence of the t allele, Lewontin and Dunn have devised a theory which postulates the acquisition of t alleles from migrants. This, unfortunately, is in conflict with the demonstrations by Dr. Paul Anderson (personal communication) that strange mice rarely, if ever, penetrate isolated populations of their kind.

There remains the question of how the patterns of social behavior that integrate and regulate the size of vertebrate populations may have evolved. To the extent that the persistence of observed patterns of behavior is a measure of their evolutionary success, it would appear that populations whose members reproduce at a rate which can be regulated are at an advantage in comparison with populations whose members all reproduce at the greatest possible rate.

A great deal of evidence supports this conclusion. Since Darwin's time, it has frequently been observed that most wild populations of vertebrates tend not

to use their food resources to the full. Growing interest in the efficient utilization of natural resources, especially in the last three or four decades, has lent experimental support for the belief that there is an optimum level for the exploitation of resources, and that this entails something less than maximum utilization. Exceeding this level may lead to the total destruction of food supplies. The ways in which vertebrate populations can be regulated and restrained from growing amidst plenty may reflect the adaptation of their patterns of social behavior to certain levels of underutilizations. Hierarchical and territorial patterns of social behavior enable the activity of an entire population to be directed towards these ends.

Clearly these patterns of social behavior represent adaptations which could have arisen and which are meaningful only at the level of the population. They apply to the activity of populations, and act primarily to ensure the fitting together of the group and the environment. Thus they serve to enhance the success and good health, or fitness, of the population.

Fitness

The success of self-regulation based on these patterns of social behavior requires, however, that individuals—often, many individuals—must be ready to give up their own reproductive potential and even survival. The success or fitness of vertebrate populations thus seems to depend on the subordination of the so-called “Darwinian fitness” of many of their members. It might appear difficult to conceive that such altruistic group attributes could have evolved in the selfish egos of individuals; if, however, the group or population did not function better than individuals, the evolution of populations with their integrative and self-regulatory mechanisms surely would not have taken place. This, of course, points again to the existence of populations as real units in biology and in evolution.

Human beings are vertebrates, of course, and human populations are also organized by patterns of social behavior incorporating particular standards of status. These patterns and standards clearly influence the breeding structures and gene frequencies of particular populations. The same patterns are

often related to processes that may affect a human population's prospects of growing or declining in size. Man alone, of course, has the potential ability of consciously regulating many of the processes that determine the sizes of his populations.

In the past human populations have not only recognized the need to limit their size but have often implemented this awareness by means of suitable social conventions. Studies of so-called primitive groups and of others, such as Eskimos, living in extreme physical environments, have revealed social acceptance of, and adherence to, practices such as sexual abstention, prolonged lactation, abortion, and infanticide, all established in order to restrict population. Among these groups numbers are not usually limited by food shortages but by social practices. Starvation is rare, suggesting that these populations, too, are geared so as not to overtax available resources. The stupendous technological achievements of man seem to have obscured the need for conservation of resources by means of social practices that restrict numbers.

Population theory as it applies to humans is couched almost exclusively in social, cultural, and economic terms. But man also belongs to the vertebrates and it is perhaps worth while at least to speculate about the possibility that some of the more purely biological or biosocial, but subcultural, mechanisms found in subhuman vertebrates may also occur in man, and so influence the dynamics of human populations.

To what extent, for instance, does population density impinge on man's highly developed neurosensory receptors and thereby affect his reproductive physiology? There are well-known fertility differentials between urban and rural areas. Though these differences are usually interpreted only in social and economic and cultural terms, it is possible that the different densities of people between country and city also contribute indirectly, and subsocially, to the lower reproductive rate of city dwellers. Even some of the well-recognized destructive effects of social tension on human health may be interpreted as homologous to the integrative and self-regulatory mechanisms which are adaptive for subhuman vertebrates, enabling them to regulate their population sizes and thus to survive.

IS THE LITERATURE WORTH KEEPING?

BY JOHN MADDUX

Scientific authors pay so little attention to literary values that their literature does not serve its ostensible purpose of intelligible, professional communication.

THOUGH IT IS fashionable to worry about the preservation of the increasing volume of scientific literature, comparatively little attention has been paid to the more fundamental issue of whether, in its present form, the scientific literature is worth preserving at all. By now, of course, it is well known that the volume of the published literature increases every year. The number of journals current at any time, and the number of papers contained in them, as well — no doubt — as the weight of paper used in their production, are exponentially increasing functions of the time and have in this spirit been widely regarded as indices of the continually increasing growth of scientific activity. Because there are more scientists and because the product of a scientist's work is a series of scientific papers, is it not natural that more papers should be published?

This argument conceals a smug indifference to the true condition of the scientific literature. With its aid too many professional scientists conclude that it is not for scientists but librarians to undertake the management of what has been called the "Information Crisis." If it should be, and it very frequently is, that one scientist finds it easier and quicker to repeat a colleague's experiment than to make an appropriate search of the literature, the blame tends

to be laid at the doors of those whose job it is to make catalogues and cross references. To be sure, the librarians are supplied with plenty of technical advice, with glossaries of technical terms, and with instructions that show how computers not yet designed may be used to make rapid searches through catalogues still to be compiled. Unfortunately, the technical community is much less ready to provide the kind of self-critical domestic help that would soften the edge of the apparent crisis by suiting the scientific literature more properly to what should be its essential purpose of communicating information and understanding between literate people.

Ponderous

By its meek acceptance of the ponderous accumulation of the current literature, indeed, the scientific community has lent support to the somewhat Freudian view that scientists, collectively as well as separately, have come to regard this mountain of printed paper as their primary product. The joke about the university department in which promotions are determined by the weight of a man's published papers is too true to be very funny. In many laboratories reprints are displayed much as if they were campaign medals on show in a general's drawing room. Among the profession as a whole there is more than a sneaking tendency to suggest that there can be very little wrong with the condition of science if the volume of its product is too great to be assimilated. In other words, the crowded library shelves are sometimes held to be a proof of productivity. Yet the arithmetic by means of which a midwestern farmer might claim efficiency by pointing to the overfull silos does not legitimately apply in the in-

tellectual field. To the extent that science is a part, and an important part, of the intellectual activity that constitutes the culture of the modern world, the incomprehensibility of much of the scientific literature is akin to a confession of failure.

To many of those who spend more time in libraries than laboratories it must often seem that the obscurity of much of the literature rests on a foundation of confusion about the purpose of papers in the scientific journals. To be sure, all scientific authors seem to be deeply, and properly, convinced that publication is an essential part of scientific activity. Failure to publish the results of a series of experiments is considered to be as serious, or even more serious, a breach of the conventions as a failure to calibrate measuring instruments, or to keep proper controls in an experiment with living things. So that papers shall be sent off to the journals, vacations may be delayed or even canceled altogether; journeys to conferences abroad may be curtailed or even abandoned; and it is a fact of common experience that working scientists stay up late, and work week ends, and worry a great deal, so that a proper record of their laboratory work shall appear in some scientific journal. To tell from the contents of the journals, however, there is very little evidence that authors actually consider their papers to serve any other purpose than that of a factual record of work accomplished — a kind of superior laboratory notebook.

Obscure

In this sense the scientific literature occupies a special place among writing. While most kinds of authors write so as to enrich their readers with some information or collection of information considered to be particularly illuminating, or so as to argue the correctness of some cherished opinion or interpretation, many scientists seem to be moved to write first for themselves and only second for their readers. The consequences of this are apparent in the character of a great deal of the published literature. Most papers are needlessly difficult to understand. Some take more time to read than their authors can have spent in writing them. Even a great many of those papers which are not obscure because of some obvious impediment, such as the construction of English sentences on the German pattern, may be

hard to grasp because their authors have puritanically confined themselves to a featureless recitation of statements from which it is only possible to pick out the striking and the remarkable on the seventh or eighth reading.

Writing of this kind leans heavily on the assumption that truth will speak for itself and, indeed, many scientists argue that a paper may be spoiled if its author appends to a sober catalogue of facts anything that smacks of being a tentative attempt to suggest what these facts may mean. It is hard to believe that modesty of this kind, at least in the exaggerated forms in which it is sometimes practiced, can be in the best interests of science. Certainly it is a modern development. Traditionally, authors wrote scientific books and papers because they wished to persuade others of the correctness of some understanding of the natural world. Far from believing that absolute truth must reveal itself, the old people had no misconception of the need for artistry and delicacy in the presentation of their scientific arguments. What, after all, is literature for but to persuade the skeptical and to convince the doubters? By now there are ample precedents to illustrate that it is not necessary to distort the truth when literature is used as a means of broadening man's understanding of the natural (or any other) world. In a period when the pace of scientific activity is quickening every year, and when scientists themselves argue in public and before Congress that their goal is to forge some deep understanding of the natural world, it is a paradox that a great part of the scientific literature seems to have been written without much concern for the elementary need to communicate understanding to other people.

To judge from the reading of the scientific journals, solicitude of this kind for what should be the purposes of literature is now exceedingly uncommon. It is rare to find a paper which has evidently been written from a wish to share with other people the excitement of some intellectual discovery. More commonly it is plain that an author has forsaken altogether the wish to communicate with the readership of the journal in which his paper appears. He may be writing for himself, for his employers, for his competitors, for the librarians, or perhaps even for posterity. With alarming frequency, there is no



This day's accumulation at the New York Public Library shows that scientific libraries are not alone in their storage problems.

evidence that he may be writing for his readers.

Inevitably a literature which is in general as flaccid as the current scientific literature must be one in which it is difficult to tell which papers are substantial contributions to understanding, and which are but trivial documents. Indeed, the evolution of stereotyped formulae for the planning of papers, and the growth of a pompous Latinate language to go with it, seem to have made it possible to clothe the results of trivial work in high-sounding trivial language. It is for specialists working in specialized fields to say how serious abuses of this kind may be. The condition of the literature has however made possible another kind of abuse which is, unfortunately, plain for all to see. Nowadays, especially in fields where progress is rapid, there is an unresisted temptation to rush into print before there can have been time to appreciate whether a piece of research has profound importance or no importance at all. Inevitably, the result is a paper which means even less to the public than to its author. Sometimes there is spawned a whole string of interdependent papers which ap-

pear as if they have been written for succeeding issues of a journal much in the manner in which newspaper correspondents are forced to meet recurring deadlines.

Compared with issues like these, it may seem unimportant that scientific papers are frequently written in a language that is a loose and even misleading imitation of that used in other forms of writing. Even so it would be wrong to count the literary style, or lack of style, of the scientific literature as a secondary matter. On the contrary, there is every reason to consider that the evil constructions which abound in the pages of the scientific journals are, as it were, the microscopic embodiment of the ill-health of the literature as a whole. For though there is no question that the language used to describe what may be, after all, the highest achievements of the Twentieth Century is matched in inelegance only by the more tedious forms of civil service composition, it cannot be inferred from this that most scientists are illiterate. On the contrary, there are people who will read Faulkner for fun, or sit hugging their delight through

a performance of Shakespeare, and who will then solemnly scatter bad language through the pages of the *Physical Review*. It seems as if the literary style of science is a convention eagerly embraced by the profession, and as if it is a convention which makes possible a great many of the evident defects of the current scientific literature.

Only welcome by the profession can reasonably explain the persistence of evil habits of style long after their existence has been diagnosed and denounced. By now there is a well-known list of literary malpractices in the scientific literature, and no sign that these are being abandoned. Thus scientists will write in the passive for paragraphs on end, with all the flabbiness that that entails. The magisterial (or is it the royal?) *we* still makes a great many scientific papers read like medieval proclamations. Infinitives are split not merely without feeling, but in ignorance. The tenses of verbs are changed for variety, and without care for their meaning. Intransitive verbs are made transitive. Everybody is his own etymologist, and almost overnight the acronym LASER becomes the noun *laser* and, finally, the verb *to lase*.

Imprecise

The most unexpected attribute of the language of the journals is its imprecision. Though most authors would be affronted by the suggestion that they might have been guilty of imprecision in the laboratory, they seem not to fear the charge of laxity at the typewriter. At least, only this can explain how some words are seized upon to embrace a whole constellation of different concepts. The noun *level*, for example, does service for a number of other words such as *height*; *degree* (as in "level of competence"); *size* (as in "population-level"); *yield* (as in "harvest-levels"); *intensity* (as in "light-level"). The same word is also used as a kind of grace note in the well-worn expressions temperature-level, obesity-level, height-level, and the like. It needs only a little more of this for the strict meanings of the displaced words to become atrophied, and for the English vocabulary of science to shrink still further.

A curious blend of telegraphic economy and wastefulness is also commonly to be found in the language of the journals, chiefly as a result of the

widespread habit of linking together pairs or larger groups of words to form a phrase of jargon. For example, among those accustomed to use *level* whenever possible, the phrase *temperature level* seems an economical way of writing *level of temperature* and so becomes a unit almost as indivisible as a single word. Inevitably, however, the point in a narrative is reached at which some change of temperature must be recorded, and then there is spelled out a phrase constructed along the lines of *the temperature level attained a new level*. To be sure, this gross assault on sensibility might well give pause to authors otherwise convinced that only Shakespearean ink could flow from *their* ball-point pen, yet tortuous and circuitous constructions like these spatter the literature, and thus help to create the illusion that much of the prose of science is really only a clever way of stringing together words so as to convey no meaning. In reality these devices, though they are frequently dismissed as mere inelegance, are grievous impediments to understanding. Not merely are they hard to disentangle in themselves, but they sap the reader's will to persevere.

Less frequently castigated faults also abound in the scientific literature. There is, for example, the curious but almost universal practice of starting a scientific paper with a resounding banality. "The translation of a four-letter nucleotide code into a twenty-'word' amino-acid dictionary has been the subject of much speculation." "The problem of which bases of messenger or template RNA specify the coding of amino-acids in proteins has been largely elucidated by the use of synthetic poly-ribonucleotides." These are the introductory sentences of articles chosen at random from a recent issue of a journal (also chosen without malice). Both of them suggest (though not conclusively) that the article that follows has something to do with molecular biology. To molecular biologists they are both statements of the obvious, and to others they may have no meaning at all. To be sure, they are convenient stretches of type upon which to append the little numbers which refer to the bibliography at the end of the articles, but they are also forbidding foretastes of the weight of unpalatable prose that follows. More than goodwill, or idle but intelligent curiosity, is needed before most readers can surmount the ob-

stacles to be found at the beginning of most papers.

But may not dullness be unavoidable in the writing of scientific papers? This is a common defense of the character of the current literature. Better to be accurate than elegant. Better exhaustive than incisive. The authors of a great many dull papers shelter behind homilies like these, and so make virtues of their failings. Yet in reality there is no reason why a paper should not be accurate and yet written in acceptable prose, or why it should not at once be exhaustive and incisive. All that is needed is the will to endow the manuscript of a scientific paper with all these desirable qualities, and others besides. To be sure, all this would require that most scientific authors should be ready to write what they mean more directly than at present. It would be necessary, for example, to abandon coy phrases such as "difficult to reconcile with" as an expression of an author's conviction that his experiments conflict with somebody else's, but that would only be yet another step in the right direction.

Irrelevant

If, however, there is no reason why the scientific literature should not be written well and in a manner that can be more easily understood, who is to be blamed because the volumes fast accumulating in the libraries fall so far short of this ideal? The librarians, perhaps? Or the schoolteachers? Or the pace of scientific change? Or the system by which research contracts are awarded most easily to research teams that publish a great deal at a great speed? Each question suggests a potential scapegoat, and there are more besides. None of them, however, substantially mitigates the offense against the best traditions of intellectual life that the present condition of the scientific literature embodies. And, as for blame, there is no question that the responsibility rests with scientists, readers as well as authors, and with the scientific community at large.

So what is to be done? Obviously it would not be practicable to send every working scientist back to school to relearn English grammar, and in any case there is no particular reason to think that drastic steps like these are either necessary or sufficient. There is, after all, the precedent of those who write obscurely only when they are writing science and

this suggests that an author's attitude towards his manuscript is more important than his acquired skill. Nothing can better a frame of mind in which he deliberately designs his paper so that it can be read without impediment not merely by his peers in the same speciality, but by his students and by men who work in related disciplines. Ideally there should be a determination to see that the intellectual content of a paper shall not be adulterated by irrelevancy, or by padding, or by deliberate obscurity, as it is in so much of the current literature.

Impatient

All of this takes time, of course, and yet scientists are the most impatient authors. Though a professional writer, a novelist perhaps, may spend a whole day making sure that a thousand words have their intended meaning, scientists begin to complain if they cannot finish writing their latest paper in a week or so. The second draft is usually regarded as a kind of martyrdom. In general it is considered that time spent writing is time taken from the laboratory and thus lost forever. It takes great strength to confess, though some do, that the process of writing a paper can actually be a salutary means of clearing the head. But in any case, because the communication of scientific discovery is so much a part of the scientific process, it is foolish to begrudge the time spent on it. Perhaps the saddest of all the qualities of the published literature are the obvious marks of haste in composition which abound.

Individuals, of course, can do no more than put their own houses in order, for there is unfortunately no inverse of Gresham's Law to arrange that the good currency should drive out the bad. So it is that the major responsibility for the condition of the literature falls on the scientific community as a whole, and on its institutions such as the learned societies, the universities, and the public laboratories. Of the many things that might be done, some cry out for urgent attention.

So far as presentation is concerned, perhaps the greatest need is that some attention should be paid to the techniques of editing scientific manuscripts. As things stand, very few journals appear systematically to require that publications shall be comprehensible. To be sure, referees are usually asked to

pronounce upon the literary merit of a paper submitted to them for professional review, and it is known that some referees reject some papers on grounds such as these. More frequently manuscripts are returned to their authors for rewriting. Most commonly, however, the acceptance of manuscripts for publication turns on their scientific virtues, and literary questions arise only marginally. Certainly no other order of priorities could account for the appearance in the journals of great numbers of badly written papers. It is only fair to recall, of course, that referees are commonly chosen for their professional expertise, and that they may have no flair and no interest in the manner of presentation.

Intelligible

But does not editing imply that one person puts words into another's mouth, and does not this entail that the editing of scientific manuscripts must lead to misrepresentations of an author's work? This seems to be the most common rebuttal of the claim that more should be done to prepare scientific manuscripts for publication, but it is itself a misrepresentation. In reality, of course, it is impossible for one person to rewrite the work of another without introducing errors and without losing nuances of meaning perhaps unconsciously incorporated into the original manuscript. Obviously it is unthinkable that the scientific journals should be equipped with rewrite teams for all the world as if they were pale shadows of *Time* magazine.

It does not, however, follow from this that there is nothing to be done for the journals by properly conceived processes of editing. In other fields, on newspapers or magazines, for example, editing at its most constructive consists of discussion between an author and a person who serves principally as an independent critic, and as a touchstone of what may be intelligible. If there have to be new words, they are the author's and not the editor's. Nuances are not lost, but gained. There is no reason why attempts should not be made to improve the intelligibility of scientific papers by similar means, though equally there is no guarantee that decisive improvements could be achieved with the kinds of resources that the scientific journals have at their disposal. Certainly the kind of detailed discussion that would be

likely to benefit authors would entail that journals should substantially increase their permanent staff, and this would be expensive. The fear that discussions of the intelligibility of manuscripts would substantially delay the publication of manuscripts is, on the other hand, exaggerated.

Obviously the value of a scheme of this kind for the constructive editing of scientific papers cannot be assessed without practical experience. It is also possible, of course, that there could not be found enough people with the interests and skills needed for a proper supervision of the character of the scientific literature, though here it is plain that recruitment would be easier if the scientific community were openly to recognize its responsibilities. But a deliberate experiment to explore the virtues of scientific literary editing could also test the value of some of the devices by means of which other kinds of literature are made plain or palatable to readers. In this context there is, of course, at present no cause to reject the possibility that the scientific literature would be easier to understand if journals were equipped with headlines similar to those found in newspapers, or with explanatory diagrams borrowing from the skills of the magazine display artists.

Ingenuous

There is no great difficulty in thinking of editorial devices of this kind that seem entirely out of character with the scientific literature as it has evolved over the years. This does not however mean that experiments should not be made. There is, indeed, a strong case for asking that some institution, and preferably one of the learned societies, should take the lead in a search for some vastly improved method of presenting scientific information to a scientific readership. The condition of the literature at present is, indeed, so bad that it may well be that most changes would be improvements. Certainly it is ingenuous almost to the point of dishonesty that the scientific community should so persistently badger the librarians for more and more elaborate methods of cataloguing the scientific literature, and for more and more storage space, when it cannot be seen to be doing everything that needs to be done to make the torrent of literature intelligible outside the narrowest of circles.

INSTITUTE RECORD

The *Rockefeller Institute Review* will be published six times a year, and will supersede the *Rockefeller Institute Quarterly*, the last issue of which appeared at the end of 1962. The new journal is intended as a vehicle for the opinions and the ideas of members of the Faculty and Graduate Students at the Institute. It will also include a brief record of events at the Institute. The *Review* is published at the Rockefeller Institute Press and is edited by Mr John Maddox. Design and layout is by Mr Reynard Biemiller. It is planned to appoint an editorial committee to oversee the contents of the *Review*.

Contributions

Contributions are invited from members of the faculty and students of the Institute. Articles should be shorter—and preferably much shorter—than 4,000 words, and should deal with matters likely to be of general interest to groups of readers similar to that at the Institute. Comments on articles appearing in the *Review*, in the form of letters to the Editor not longer than 500 words, will also be considered for publication. The contributors of the articles in the current issue are Alexander Kessler, a physician who has been a graduate student at the Institute since 1961, and John Maddox, Science Editor of the *Manchester Guardian*, now an affiliate of the Faculty of the Rockefeller Institute.

Television Setting

The Caspary Auditorium will be the setting, in February, for a series of five television programs produced by CBS News under the general title "The Great Challenge." Among the issues to be covered by the series of discussions is the question of how far the federal government should participate in education; the problem of the increasing gap between the "scientific elite" and the rest of society; the place of the federal government in the regulation of the country's economy; the possibility that the arts may be neglected in modern society; and the opportunities for individual self-expression in modern society. For the second pro-

gram in the series, on February 10th, the list of participants announced by CBS News included Dr Jerome Wiesner, Dr Detlev W. Bronk, Dr George Wells Beadle, and Mr Gerard Piel.

Laboratory Tours

By the end of January 1963 no fewer than thirteen demonstrations had been held by individual laboratories at the Institute as part of the program whose purpose is to provide students and members of the faculty with an opportunity to learn of research currently under way. The program began at the end of November, when Professor George Palade held court in the South Laboratory. According to the Dean's Office, which administers the program, the audience at the several demonstrations has fluctuated from fifteen to well over forty. By now the procedure at the demonstrations seems to have settled down to a uniform pattern. A short introductory talk by the head of the laboratory on show is followed by a guided inspection of work in progress. The demonstrations usually take place on Mondays and Thursdays each week.

Christmas Lectures

There was a full attendance at the Caspary Auditorium for each of the four lectures in last year's series of Christmas Lectures for young people. The subject of the lectures was "Chance and Regularity," and they were delivered by Professor Mark Kac. The demand for tickets from high schools in the metropolitan area outstripped even that experienced in past years. Elsewhere in the country the themes of the first three series of Christmas lectures to be held at the Institute were reused by their original authors for the benefit of audiences of young people. Thus Professor Paul Weiss lectured at Seattle, Professor René Dubos at Chicago, and Professors Lyman Craig, Stanford Moore, and William Stein at Boston. These lectures were part—and, indeed, the whole part—of a program sponsored by the American Association for the Advancement of Science. Finan-

cial support for the venture was provided by the National Science Foundation.

Christmas Festivities

Christmas Festivities at the Institute were lent a seasonal air by the cold weather, which, among other things, made it possible to turn the esplanade above the 68th Street car park into a skating rink. The graduate students entertained the Faculty and Trustees at their annual dance on December 15th; the party for children was held on the evening of December 19th and more than 600 people, including faculty, students, and employees of the Institute, joined President and Mrs Bronk in Welch Hall for the annual Carol Singing on December 20th. On the day after Christmas CBS News used the Caspary Auditorium for the presentation of their annual TV program "Years of Crisis." On New Year's Day President and Mrs Bronk dispensed eggnog.

Caspary Dome

The blue marble tilework has now been stripped from the external shell for the Caspary Auditorium, and for the time being the underlying concrete has been painted white. Though the Fuller Construction Company's men worked for several days on this awkward hemispherical surface, the work was done without accident. Architects are now working on plans for the reconstruction of the dome.

Travelers Abroad

Travelers from the Institute include Dr Detlev W. Bronk, who will attend the United Nations Conference on the Application of Science for the Benefit of Less Developed Areas to be held at Geneva, February 4th through 19th. Professor René Dubos will read a paper at the same conference. Professor Alfred Mirsky and Dr Stanford Moore will both attend a symposium on protein chemistry to be held in Madras, India, and afterwards Dr Moore will continue a journey that will eventually carry him all the way round the world. Among other things he is to lecture in Israel, India, Japan, Hawaii, and California. At the same time Professor Theodosius Dobzhansky and Mr Thomas J. Tidwell have gone to Central America to collect samples of the wild populations of species of *Drosophilae*.

Electronic Computers

The reputation of the Institute as one of the last establishments of its kind without an electronic computer on the premises has now been destroyed, for Professor Keffer Hartline's laboratory is now equipped with a desk-sized machine. The computer has been bought with the help of a grant from the U. S. Public Health Service, and Professor Hartline is using it for the analysis of signals in the optic nerve. Apparently it has been possible to connect experimental nerve tissue directly to the computer, so that there is no need of special arrangements for feeding information into the machine.

Amor Musicae

On Sunday December 16th, in the Caspary Auditorium, *Amor Musicae* gave a performance of the concert version of Handel's "Acis and Galatea." Mrs Reba Mirsky, wife of Professor Alfred Mirsky, played the harpsichord.

Holistic Biology

A series of seminars in "holistic" biology will be held at monthly intervals during this academic year, and the first of them was addressed by Professor George Wald, of Harvard University, on the evening of January 9th. Usually it is intended that speakers shall dine with their audience before the proceedings proper, but the demand for places at the dinner for Professor Wald was too great to be met in full. Dr Bruce Voeller, who is organizing the symposia and declines to commit himself to a formal definition of "holistic," says that future plans include talks on subjects such as the migration of birds and fish, and the relationship between the various routes to the understanding of evolution.

Faculty Appointments since 1 November 1962

RESEARCH ASSOCIATES

ENOCH GORDIS (Professor Dole)
Former Guest Investigator.

MARCUS A. HAIRSTONE (Associate Professor Dan H. Moore)
Former Assistant Professor, Long Island University.

ZULEMA J. SABATINI (Professor Hotchkiss) Former Guest Investigator.

Guest Investigators arriving since 1 November 1962

E. G. D. COHEN (Professor Uhlenbeck)
Associate Professor, University of Amsterdam, The Netherlands.

MICHEL FOUGEREAU (Assistant Professor Edelman) Fellow, Comité de Biologie Moléculaire, Paris.

RALPH E. SCHROHENLOHER (Professor Kunkel) Assistant Professor of Medicine and Instructor in Biochemistry, University of Alabama Medical Center, Birmingham.

EDUARDO TORROJA (Professor Dobzhansky) Fellow, Spanish Research Council.

Departures from the Faculty since 1 November 1962

ASSISTANT PROFESSORS

RICHARD M. FRANKLIN left in January to become Associate Professor at The University of Colorado School of Medicine, Denver.

SEYMOUR J. KLEBANOFF left in November to become Associate Professor of Medicine at the University of Washington, Seattle. He will continue to be associated with the Institute as a Guest Investigator.

RESEARCH ASSOCIATES

JORGE E. ALLENDE left in December to return to the Instituto de Química Fisiológica in Santiago, Chile.

RUTH ARNON left in January to return to the Weizmann Institute of Science, Rehovoth, Israel.

SIWO REL DE KLOET left in December to return to the Van't Hoff Laboratory of the University of Utrecht, The Netherlands.

PER CHR. HEMMER left in December to return to the Institute of Physics of the Norwegian Institute of Technology in Trondheim.

MARIA TOMASZ left in November to join the Department of Biochemistry of New York University College of Medicine.

EWALD R. WEIBEL left to return to the Department of Anatomy, University of Zurich, Switzerland.

Guest Investigators leaving since 1 November 1962

E. G. D. COHEN left in January to return to the University of Amsterdam, The Netherlands, where he is an Associate Professor.

STUART D. ELLIOTT returned in January to the University of Cambridge, England, where he is Assistant Director of Research in the Department of Animal Pathology.

ROBERT L. KIRK left in January to return to the University of Western Australia in Perth, where he is Reader in Human Genetics.

HENRYK PANUSZ returned in December to the Department of Physiological Chemistry of the Academy of Medicine, Lodz, Poland.

EDITH WIENER left in December to return to Hebrew University Hadassah Medical School Laboratory of Microbiological Chemistry, Jerusalem, Israel.

F. PETER WOODFORD left in December to return to the Department of Physical Chemistry at the University of Leiden, The Netherlands.

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ILLUSTRATIONS

COVER PHOTOGRAPH: Hanging stairway leading to esplanade from north end of campus, by Stephan Pischinger. PAGE 3: Wall Street noon crowds, U.P.I. photograph; colony of mice, The Rockefeller Institute Illustration Service. PAGES 6 AND 7: animal photographs courtesy of South African Tourist Bureau, sea lions courtesy of the American Museum of Natural History. PAGE 11, courtesy of The New York Public Library.
