Ecology and Population

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Man's occupance of the earth is everywhere under attack by environmentalists and conservationists. Man is harassed for using nature's resources, for building dams, for exterminating bothersome species, for disposing of his refuse, for using the waters, for cultivating the topsoil, for employing insecticides, and for just being present. One gets the impression from this cacophony that nature has been contrived for all species of life except man. Even the ecologists, who should know better, belabor man with an environmental rhetoric that fails to acknowledge the many parallels between the behaviors of populations of lower and higher forms of life. It is possible that such statements as "man is a shocking biological innovation," "man is in conflict with nature," "population growth causes a disproportionate negative impact on environment," and "urbanization is a cancerous growth" may serve a useful purpose in the campaign to bring about a more sensible use of resources and environment. But since these colorful statements are put forth in the name of ecology and in the interest of solving the population problem, there is reason to enquire into their accuracy. What, in other words, is ecology, and what is its contribution to population study?

Ecology, as commonly defined, is the study of the relation of organism to environment. Inasmuch as organism and environment make up all of nature, ecology would seem to be the study of the relation of everything to everything else. An undertaking of that scope is manifestly far too ambitious to be very productive within specifiable intervals of time. Some sort of limitation of the subject, arbitrary though it may be, is essential if anything is to be accomplished during a scholar's lifetime. The holistic approach, moreover, when held too rigidly, leads to a disappearance of variables; every property tends to be seen as an aspect of another property. On this score, too, expediency must be consulted. Despite these inherent difficulties, an approach that attempts to deal directly with complex wholes is a useful complement to the usual analytical treatment of actual events.

The scaling down of ecology to manageable proportions proceeds along either of two lines. One is represented in studies of relations between given species and particular environmental features. Problems of the effects of variations in light on the reproduction of a plant species, of the relation of vegetative cover to the nesting habits of ground-nesting birds, and of the effects of a parasite on its host are illustrative. A second kind of limitation is what might be called a systems approach, as exemplified in attempts to analyze the interactions among a set of species in the process of adapting to their environment. Studies of this type represent the ecological point of view most fully, although they are not the most common.

The clearest illustration of the systems approach in ecology is found in the uses of the ecosystem concept. This has been set forth succinctly in a recent paper by Eugene Odum, who says that an ecosystem ". . . is considered to be a unit of biological organization made up of all of the organisms in a given area (that is, "community") interacting with the physical environment so that a flow of energy leads to characteristic trophic structure and material cycles within the system" (*1*, p. 262; *2*). The community-environment interaction as thus described takes the form of a developmental process known as succession. In that process, each association of species (that is, community) alters the chemical and sometimes the physical characteristics of a unit of territory through its occupance of the area, thereby preparing the way for its displacement by a succeeding association of species, and so on. After two, three, or more such stages, the process culminates in a climax stage, which comprises an association of species that can maintain itself indefinitely in the area. The climax stage is described by Odum as one in which the "maximum biomass (or high information content) and symbiotic function between organisms are maintained per unit of available energy flow" (*1*, p. 262). In short, succession is directional, developmental, and predictable; it is the ontogenetic counterpart of biological evolution (*3*).

As a theory, the concept of the ecosystem is attractive. It is simple in design, it appears to identify and describe a unitary phenomenon, it indicates how structure might be a predictable outcome of change, and it suggests the possibility of forecasting the population size of a mature biotic community. Its virtues, however, are also its limitations. For example, viewing the environment as a specific unit of territory seems inadequate. It is hard to believe that the organisms in adjacent territory are without effect on events in the area marked off as environment. Nor is any information given concerning the species displaced in the course of succession. Furthermore, the equilibrium attained in the climax phase of succession is allowed to stand without qualification; perhaps the balance of numbers in the several species and the balance of the entire community with energy resources in the environment should be regarded as a process rather than as a stable state. The tendency of animals to multiply to the maximum carrying capacity of their habitats has not been clearly established in reports on their territorial habits. However, every abstract formulation neglects or obscures a great amount of information in the interest of parsimony: presumably, important substantive issues are taken up as the occasion arises.

The more pertinent question of the moment is, What relevance does the ecologist's concept of the ecosystem have for mankind? On this point there seems to be no small amount of inconsistency. Many environmentalists who profess an ecological point of view are inclined to exclude man from ecosystems. Although they may acknowledge that all of life is interrelated, they nevertheless look upon the human species as a sort of apocalyptic force

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thrust upon nature from some anti-nature. Their ambivalence is whimsical, to say the least. While man is being buffeted with criticism for his misuses of the environment, there is silence on the activities of beavers that cut more trees than they need, on the animals that trod out pathways which become channels of erosion, and on various polluting effects of animal behavior. Evidently there is a beneficent homeostasis that operates to correct the depradations caused by lower forms of life, but not those of man. It is also strange that many species can disappear through excessive inbreeding or some other error in animal judgment without bringing on ecological catastrophe, yet the threatened elimination of the bald eagle or the jaguar is a disaster of major proportions. Eutrophication, that word with the curiously inverted connotation, turns out to be no more than an esthetic tragedy, unless nature doesn't really set as high a value on green plants as we have been led to believe. This confusion of personal preferences, esthetic predilections, and moral judgments with scientific principles can hardly be of service to ecology.

Professional ecologists, on the other hand, show a much greater willingness to include man in ecosystems whenever it is appropriate to do so. They often err in another direction. That is, they tend to treat man simply as a species, as an aggregate of homogeneous individuals rather than as a highly differentiated and organized population. This viewpoint may result from the biological perspective that dominates most ecological work. The great strides that have been made in adapting demographic techniques to plant and animal population studies have not been matched by an awakening to the effects of social and economic structure on the man-environment relationship.

Of central importance in appraising the applicability of the ecosystem concept to human society is the design of the concept itself. It will have been noted, no doubt, that it is almost an exact replica of the Malthusian model. There is the notion of a specific unit of territory with fixed resources, an irresistible tendency for organisms to multiply to the maximum carrying capacity of the resources, the emergence of an equilibrium of numbers with resources at a subsistence level, and, finally, an implicit assumption, by virtue of the subject matter, that all other possible variables are constant. Both the ecosystem in Odum's hands and the Malthusian theory are analytical constructs.

There is nothing wrong, of course, with an analytical model, as long as its use is confined to the purposes for which it was constructed. That, unfortunately, has not been the experience with either the ecological or the Malthusian form of the ecosystem concept. The all-important limiting assumption of a fixed state of the art has lulled many people into either forgetting that the state of the art is a variable of consequence or believing that the variable has been neutralized to the point where environment is the determining factor in population growth. Hence the model has been freely employed both as a description of actual situations and as a diagnosis of societal problems.

The Malthusian conceptualization of the man-environment relationship is widely favored, especially by biologists and others who have had little or no exposure to modes of thinking in the social sciences. Garrett Hardin, for example, thinks of human population in a simple-minded analogy with grazing animals in a fenced pasture (*4*). He measures current population trends against "foreseeable technology," by which he means an unchanging technology. His is a view that has been informed by neither a historic perspective nor a competent assessment of the existing informational and institutional resources for change. The Malthusian model also supplies the major intellectual underpinning for a great deal of contemporary family planning ideology. Wherever it is assumed, by action if not by explicit statement, that population is the only factor which can be expected to vary, or which can be manipulated, one finds an iteration of the classical view. Popular scientific literature is full of oversimplified explanations of pollution of malnutrition, of poverty, and of psychological tensions in cities.

Constructions other than Odum's can be put on the term "ecosystem." Odum's is a system with boundaries determined by the physical limits of a settled population, a definition that may be appropriate for plants, but not for animals. The more general use of the term is in reference to systems with boundaries delineated by the outer reaches of functional relationships—that is, by the circulations of energy-producing matter rather than by place of occupance (*5*). On this basis, ecosystems vary greatly in scope and in composition (*6*). The more diversified the food habits and other activities of an association of species, the more far-reaching and intricate its ecosystem. In this sense, the human ecosystem exceeds that of any other class of organisms. It is further complicated by the fact that human beings enter into energy cycles not as a simple aggregate, but in a highly differentiated way. For these reasons, the role of mankind in an ecosystem should be examined separately and in detail before comparisons with other communities are carried beyond the analogical stage.

It is at this point that a human ecology, as distinct from bioecology, makes its appearance. The extension of the ecological point of view to the study of *Homo sapiens* carries with it two assumptions, both of which are implicit in the concept of the ecosystem. First, adaptation to environment is an imperative and omnipresent concern for every class of living thing. Second, adaptation, in all but a few physiological respects, is a collective phenomenon; it is achieved not by individuals acting independently, but by combining their special abilities in an organization that operates as a unit of a higher order. The assumed transferability of methods and concepts from lower to higher forms of life is based mainly on the greater degrees of similarity among populations (which are the units of ecological study) than among individuals. Differences between levels of life appear, of course, in the applications of the assumptions.

The first assumption, that environmental adaptation is necessary, needs no exposition, although the pervasiveness of its implications in human affairs is not universally appreciated. There is some room for uncertainty, however, in what constitutes environment and in what the nature of the adaptive relationship is. In discussing these points, I retrace some of the ground covered by Ansley Coale (*7*). My purpose in doing so is to explore the application of ecology to population study; it is not to try to improve upon his statement.

It should be noted that the term "environment" has no fixed denotation. It is a generic concept for whatever is external to and potentially influential upon a unit under study. The environment of a population is different from that of an individual and from that of a set of populations. Thus the act of defining refers one back to the thing environed. That thing, from the standpoint of ecology, is a population which is organized or in the process of organization. The clarity of the environmental definition can be no greater than that of the environed unit.

A great deal of what is external to any entity is often overlooked in considerations of environment. The usual practice is to restrict the term to those externalities that are close by and directly experienced. While that may be expedient in some situations, the restriction is clearly arbitrary. Numerous repercussions from distant events are felt in any given locality. Still, the fact of the matter is that the content and the boundaries of environment are affected by the accessibility of the unit or by its facility for movement. Environment, in other words, includes as much of what is external as can be reached in any given interval of time. Obviously, then, both location and the transportation and communication facilities possessed by a community or society are determinants of their environment.

Where the means of movement are crude and costly, where production techniques are primitive, and where marketing facilities are nonexistent, a community lives in a narrowly circumscribed area and in intimate association with its biophysical environment. The model of the closed ecosystem is very nearly approximated under such conditions. Even so, population is regulated by the personnel requirements of the community, which may remain fairly constant over long periods of time. Instances of this kind, once rather commonplace, are vanishing from the human scene (*8*).

The disappearance of easily recognized ecosystems has followed the accumulation of human culture and the expansion of organization. I need not linger over the character of the expansion process. Dudley Duncan's "Social organization and the ecosystem" (9) leaves little to be said. It is enough to repeat here that in the long sweep of Western history the scale of territorial organization has advanced from the small, village-centered system delineated by a pedestrian ambit to the vast, urban-dominated, interregional domain knit together by various mechanical means of transportation and communication. The spreading territorial division of labor has arrayed population centers and their respective tributary areas in functional hierarchies, while extending commercial and cultural influences outward in many directions. There are now numerous large, diffuse, and multicentered urban systems that overlie and interpenetrate one another at many points. Many of the events in the West of the last two or three centuries are being repeated in the developing nations, albeit in an uneven and faltering fashion. The prospect is that the urban systems now being formed in the developing nations will ultimately fall into appropriate functional positions in the world's urban hierarchy.

Organizational expansion has produced a number of large-scale changes in the human population's relation to its environment. First, the local environment (that which is encompassed in the daily and weekly circulations of a resident population) has been converted from a source of sustenance to so much space within which nonextractive uses are arranged. In that setting, adaptation has become largely a housekeeping task. As the importance of the local environment has receded before the widening scope of the extra-local environment, land uses in the former have been regulated increasingly by events in the latter. There are other notable consequences of the enlargement of the environment. For example, each localized population now draws its food and other materials from such a wide area that an accurate description of its effective environment poses an almost insurmountable measurement problem. That problem is further complicated by frequent shifts and substitutions of resource use brought about by technological changes. A related effect of expansion concerns the extent to which the physical and biotic environment is mediated through other organized populations (*10*). The thickening web of exchange relations that has spread across the world has created a social environment between each local population and the physical environment. Much of the latter has been so effectively screened from view that it has been easy for people to acquire an attitude of indifference and neglect toward their physical world. A third effect of expansion is that the environments, both physical and social, of all human groups have become increasingly alike. Virtually everyone in the Western world can now remain at a given place and still have access to all of the world's products and all of the information available in repositories, wherever located. Environmental standardization in this sense will soon become worldwide.

It may be that this merging of societies and consequent sharing of a single environment will, as it progresses, result in some loss of adaptability and some risk to survival. Formerly, when human settlement consisted of many somewhat isolated communities or societies, catastrophe could strike one or more without affecting others. Had there been radical shifts in environmental conditions, some societies might have succumbed, while others could have successfully adapted to the change. Adaptive innovations acquired thereby would then be available for diffusion to other localized societies. Diffusion, the accumulation of innovations, expansion, absorption of people in enlarging societies, and further expansion have taken us far from the early state of adaptive anarchy. With the approach of an embracive social system, there might be no more than one chance at adapting to drastic environmental shifts and no more than one chance to survive a major upheaval.

What I have been saying in a roundabout way is that there is no direct relation between population and environment. Every population confronts its external world as some form of organization. The critical relation, then, is between an organization and environment. If there are environmental problems, their explanation and their solution must be sought in the way the given organization is constituted. It should be no less evident that adaptation is a collective (that is, organizational) achievement.

If it is true that adaptation is necessarily accomplished through organization, the fact has profound implications for the importance of the individual in the determination of societal events. His contribution to the adaptive process, it logically follows, is confined largely to his performance of a more or less specialized function in a division of labor. There are certain functions, of course, that place some individuals at the confluxes of information flows. Those few individuals have opportunities, assuming other conditions are favorable, for contributing to adaptation through invention and discovery. But in general, most of the options open to individuals consist of using or not using, or making choices among, the goods, services, vocations, and avocations generated by the same division of labor in which they are themselves involved. How those amenities are used is also determined by the structure of the system.

This seems to fly in the face of common sense. Everyone knows, from long experience as an initiator of action, that it is the individual who wills things to be done and it is the aggregate of willing that produces social phenomena. People act alike in a given situation, so goes the reasoning, because they have common values, a term that probably is translatable as common motives. But to the ecologically minded student, that proposition merely begs the question, for it leaves unanswered the question of how commonality of values or motives came into being. It would seem that, in the degree to which behavior is similar, the explanation of that behavior cannot be found in psychological variables—it must be sought in the processes involved in the operation of the social system. Individuals may expound at length on the reasons for their having a given number of children, for migrating from one place to another, or for engaging in any other kind of activity, but only a few are perceptive enough to recognize that the degrees of freedom in their decision-making are fixed in the structure of society.

Thus the belief that birthrates remain high in developing countries because people are not motivated to reduce their fertility seems to confuse a fact with its explanation. It fails to take account of the very strong probability that fertility behavior is so enmeshed in a web of institutionalized relationships and practices that it cannot be isolated for separate treatment. Even though death rates may have fallen substantially in areas undergoing modernization, birthrates tend to remain high because for most of the population the family is still the primary producing unit, the network of kinship obligations is unaltered, production continues to be labor intensive, and no substitute for the family as a source of old-age security has emerged. As long as the structural features of an agrarian society persist, it seems unlikely that contraceptive distribution programs can do more than reduce the frequency of pregnancies to what is needed to maintain a given number of surviving children per couple. The dependence of changes in vital rates on changes in the social structure has been recognized, notably by Ronald Freedman (*11*), but it has had relatively little acceptance in either research or policy spheres to date.

It is entirely consistent with this line of reasoning to infer that population problems are essentially problems of adjusting the size and characteristics of population to the personnel requirements of a social system. This may be clear enough where simple societies are concerned, but the adjustment becomes much more involved in the case of complex societies. I shall pursue one aspect of the relation of population to society, if only for illustrative purposes.

Consider the population requirements in an expanding system. The demographic transition model will serve as a useful vehicle in examining those requirements. In that context, I start with the assumption that, prior to the onset of cumulative population growth, rates of birth and death are high and in an unstable equilibrium and that the balancing of vital rates is a function of an equilibrium between population and organization. In other words, birthrates tend to adjust to mortality and thereby to maintain the number and kinds of people needed to staff an organization.

That being the case, any significant change in the manpower needs of an organization upsets the vital equilibrium. If that change is in the direction of permanent increases in productivity and in the amount of product, birthrates and death rates will move downward (death rates declining more rapidly), eventually reaching a new equilibrium at a lower rate. To reason from the transition model would lead one to believe that the new birth-death equilibrium implies a new population-organization equilibrium. If that inference were correct, the nature of the new population-organization equilibrium would be quite different from the one that is assumed to have existed before. In the developed countries, while birthrates and death rates are approximating equivalence, organizational complexity and technological accumulation continue to increase exponentially. Clearly this is an outcome that Malthus did not anticipate. It is doubtful, moreover, that it has any parallel among lower forms of life.

An explanation of the detachment of birth-death equilibrium from population-organization equilibrium is probably to be found in the operation of one or more substitution principles. Perhaps one of these substitutions involves reckoning in terms of man-years rather than in terms of number of individuals. If each live birth yields an average of 68 years of life instead of 30 years, then obviously a given aggregate number of man-years of life can be realized from fewer than half the number of births. Of equal, if not greater, importance is the substitution of capital equipment for people. In other words, it appears that in the process of technological change a point is reached at which productivity becomes independent of the size of the labor force. This may be why Simon Kuznets found negligible correlations between population growth and economic growth in the histories of developed countries (*12*). Gains in the efficiency of tools and productive organization feed off accumulated information and consequently displace increasing numbers of workers. In the United States, for example, the ratio of capital to labor has been rising at about 1.25 percent per year for the past century (*13*). It is this circumstance which lies behind the shift of industrial predominance in the economy from primary to secondary to tertiary sectors. As far as population size is concerned, it appears that a social system has an asymptotic property that is fixed by the manpower requirements of the technology in use.

But what are the manpower requirements of an industrialized society? It does appear that they are considerably higher than those of an agrarian society. A point of uncertainty in this connection has to do with what should serve as a basis for comparison. It may be observed that industrialization supports many more people in a given amount of space than did the preceding agrarian economy. Now, if more people are necessary in societies that are advancing to higher levels of productivity, then the lagging decline of the birthrate in the demographic transition was also necessary. Only thus could the increased numbers of people required to fill the growing diversity of roles be obtained; people can be born anywhere, of course, and move to the region undergoing change. Does this mean that the experience of the West must be repeated in the developing nations? Will industrialization necessitate substantial increases in the populations of India, mainland China, and other crowded parts of the world? Perhaps not. Recent population growth in those areas, out of phase though it might have been, might already have produced enough people to man a highly complex economic and social order.

The transformation to an industrialized society appears to call for a rather intricate demographic involution. Unfortunately, it has not been possible to demonstrate some of the aspects of the reallocation of manpower very satisfactorily. It is more than probable that, as industrialization advances, the proportion of the population comprising the labor force declines. But the measurement problems are such that official statistics give us only the numbers that occupy conventionally recognized positions in the economy. The data normally exclude housewives, children who perform useful chores around farm and house, and old people engaged in light tasks. Longitudinal studies on the proportion of a population in the labor force are confounded by tranfers of workers from unpaid to paid employment. A standardized enumeration of all people who participate in economies, were that feasible, would probably show relatively more people doing productive work in agrarian than in industrialized societies.

A decline in the relative size of the labor force does not, however, contradict the need for large numbers of people in an industrially advanced society. While such a society needs comparatively few workers, it needs relatively more consumers. In an agrarian society, everybody, excluding only the very young child and the infirm adult, is both a producer and a consumer, although not in the same degrees. In the industrial society, on the other hand, a large body of specialized consumers, whose economic contribution to the system is that of consumption, emerges. That includes virtually everyone under 17 years of age, a substantial and increasing proportion of those aged 17 to 22, and most people over 65. It might be argued that the product consumed by persons under 22 years of age is also an investment, but all consumption might be so regarded. The specialized consumer role, viewed as parasitic in some quarters, is vital to a highly productive economy. Unless this role is diligently cultivated, all of the goods and services produced will not be taken off the market, the scale of industry could not then be maintained, and the advantages of mass production will have been curtailed.

Several contingencies will affect the consumer function now and in the future. One of these concerns the reliance of industrial economies on foreign populations for some of the consumption needed to sustain them at efficient levels of production. The dumping of surplus products in foreign markets, ordinary trade relations, and foreign aid have served that end. But it may not be possible to depend on foreign populations to the same extent in the future as in the past. As the economies of developing nations mature to the point where they can supply their own populations with full ranges of consumer goods, their assistance in maintaining the economies of the developed nations will decline.

A possible second contingency is a decline in the ratio of children to adults. This might be thought to reduce dependency and thus contract the market for consumer durables and numerous services to households. As already suggested, however, that effect is being offset by increases in the ratio of nonworkers to workers. An estimate prepared by Juanita Krebs and Joseph Spengler indicates that, if productivity continues along the trend it has followed since the turn of the century (that is, increasing at about 2.5 percent per year), the increment in the years from 1965 to 1985 would represent an increase in per capita income of 82 percent. Or, if per capita income could be held constant and the labor force reduced instead, some 45 percent of it, or around 28 million workers, would be converted to consumers (*14*).

A third contingency that could significantly affect the consuming power of a population is governmental action aimed at substantially improving the standard of living of the disadvantaged members of the society. In the United States, the approximately 13 percent of the households that are regarded as below the poverty ceiling, or the 27 percent of households with incomes below $5,000 in 1970, offer a considerable opportunity for expanding consumption. There are numerous other ways to dispose of the excess productive capacity of the economy, such as rebuilding the urban settlement structure, cleaning up the environment, or engaging in bigger wars. To the extent that these latter alternatives are resorted to, consumption becomes independent of population size.

Enough has been said to indicate that population is not regulated by the physical and biotic environment. Although the environment may be finite, organizational determinants will come into force long before the environment itself operates as a restraint on population. The population problem is a problem of adjusting numbers and their characteristics to the demographic requirements of a particular society. If the line of reasoning followed here is correct, at some time in the course of technological and economic development population size becomes a neutral factor in the amounts and kinds of uses of natural resources to be expected. The power for technical and organizational innovation implicit in the already accumulated fund of knowledge is inestimable, and it is constantly being enlarged. The exploitation of the potentialities of that reservoir, carried on by a relatively small and perhaps declining number of specialists, means a steadily rising level of productivity and a persistent problem of how to sustain it.

I should like, in conclusion, to return briefly to the question of the contribution of ecology to population study. In a word, the contribution is the formulation of the population-environment problem in organizational terms; adaptation is necessarily an organizational process. The bioecologist might ignore this approach from time to time without getting into serious difficulty, and the social scientist may set it aside for certain analytical purposes. But neither will gain a very full understanding of population change and structure apart from the organizational context in which they occur. Thus human ecology, although it may start with an interest in the similarities among all life forms, converges upon and becomes identified with social science. It becomes, however, a synthetic social science; that is, the nature of the ecological problem is of such breadth that it cannot be adequately treated from the standpoint of sociology, economics, political science, or any other similar abstraction. Human ecology constitutes a different abstraction, one that pertains to the interrelations among institutions rather than to a single class of institutional behavior. As a synthetic social science, human ecology seems well suited to population study, for population belongs to no one discipline.

References and Notes

1. E. Odum, *Science* **164**, 262 (1969).
2. A simpler definition is offered by Lee R. Dice: "An ecologic community together with its habitat constitutes an ecosystem" [*Natural Communities* (Univ. of Michigan Press, Ann Arbor, 1952), p. 21].
3. See also W. C. Allee, A. Engerson, O. Park, T. Park, K. P. Schmidt, *Principles of Animal Ecology* (Saunders, Philadelphia, 1955), pp. 695–729; R. Buchsbaum and M. Buchsbaum, *Basic Ecology* (Boxwood, Pittsburgh, 1957), pp. 98–127; and R. Margalef, *Perspectives in Ecological Theory* (Univ. of Chicago Press, Chicago, 1968), pp. 26–50.
4. G. Hardin, *Science* **162**, 1243 (1968).
5. See M. Bates, in *Resources and Man* (Freeman, San Francisco, 1969), pp. 21–30.
6. Impressive advances in the measurement of the energy converted, lost, and transmitted at each stage of the cycling process are being made in the new science of energetics, as described by H. T. Odum, *Environment, Power*

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7. A. Coale, *Science* **170**, 132 (1970).
8. I. Taeuber [in *Man's Place in the Island Ecosystems*, F. R. Fosberg, Ed. (Univ. of Hawaii Press, Honolulu, 1961), pp. 226–262] analyzes how absorption into expanding societies affects the age and sex composition of populations in formerly isolated social systems.
9. O. D. Duncan, *Handbook for Modern Sociology*, R. E. L. Faris, Ed. (Rand McNally, Chicago, 1964), pp. 36–82.
10. K. Boulding describes the human ecosystem as the "totality of human organizations" [*The Organizational Revolution* (Quadrangle, Chicago, 1952), p. xxii] and O. D. Duncan notes that the cycling of information is a unique feature of the human ecosystem (9, pp. 40–42).
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Size and Shape in Biology

Elastic criteria impose limits on biological proportions, and consequently on metabolic rates.

Thomas McMahon

Observers of living organisms since Galileo have recognized that metabolic activities must somehow be limited by surface areas, rather than body volumes. Rubner (*1*) observed that heat production rate divided by total body surface area was nearly constant in dogs of various sizes, and proposed the explanation that metabolically produced heat was limited by an animal's ability to lose heat, and thus total body surface area. When more precise methods of measurement became available, Kleiber (*2*) noticed that when rate of heat production is plotted against body weight on logarithmic scales for animals over a size range from rats to steers, the points fall extremely close to a straight line with slope 0.75 (Fig. 1). The result has since been confirmed for animals as different in size as the mouse and the elephant (*3–5*), and has been verified for other metabolically related variables, such as rate of oxygen consumption (*6*). Excellent reviews of the problem are available (*7–10*).

While it is often true that biological laws are not derivable from physical laws in any simple sense, Kleiber's rule may be one of those fortuitous exceptions which D'Arcy Thompson (*11*) suggests lie at the basis of a fundamental "science of form." Plants as well as animals must be built strongly enough to stand under their own weight. In the following, a general rule is derived for the changing proportions of idealized trees as a function of scale, and later the results are applied to animals.

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Buckling

Consider a tall, slender cylindrical column of length l and diameter d loaded by the force P, representing the total weight of the column, acting at the center of mass. Such a column will fail in compression if the applied stress P/A, where $A = \pi d^2/4$, exceeds the maximum compressive stress, σ_{max}. Provided that the column is slender enough, it may also fail in what is known as elastic buckling, whereby a small lateral displacement (caused, for example, by the smallest gust of wind), allows the weight P to apply a toppling moment which the elastic forces of the bent column below are not sufficient to resist. In this case, "slender enough" means that l/d is greater than 25, a range which includes virtually all trees (*12*). The critical length for buckling is related to the diameter by:

$$l_{cr} = 0.851 \left|\frac{E}{\rho}\right|^{1/3} d^{2/3} \qquad (1)$$

where ρ is the weight per unit volume and E is the elastic modulus of the material. The mathematician Greenhill (*13*) showed that when the force due to weight is distributed over the total extent of the column instead of being taken as acting at the center of mass, the critical height becomes:

$$l_{cr} = 0.792 \left|\frac{E}{\rho}\right|^{1/3} d^{2/3} \qquad (2)$$

This result is identical to Eq. 1, with only a change in the numerical constant. It may be demonstrated that another change in the constant occurs when the solid cylinder is made hollow, provided that the thickness of the wall is proportional to the diameter. Greenhill further showed that if the shape of the column is taken as a cone, or a paraboloid of revolution, the result is again only to change the numerical constant. Recently, Keller and Niordson (*14*) have derived that the tallest self-supporting homogeneous tapering column is 2.034 times as tall as a cylindrical column made of the same volume of the same material, and that the distance to the top of such a tapering column above any cross section is proportional to the diameter of that cross section raised to the ⅔ power. The rule requiring height to go as diameter to the ⅔ power is thus independent of many details of the model proposed for the elastic stability of tree trunks.

Bending

The limbs of trees must also be proportioned to endure the bending forces produced by their own weight. If a branch is considered to be a cantilever beam built into the trunk, there exists a particular beam length l_{cr} for which the tip of the branch extends the greatest horizontal distance away from the trunk (*15*). Branches longer than l_{cr} droop so much that their tips actually come closer to the trunk. Suppose that the purpose of branches is to carry their leaves out of the shadow of higher branches, and therefore to achieve a maximum lateral displacement from