1

PRODUCTIVITY GRADIENTS

1-1 THE CONCEPT OF LIFE

Life is a process that involves the expenditure of energy for the redistribution of matter. This fundamental truth applies to life processes at the molecular level, to the whole organism, and to populations. The redistribution of matter or materials at the molecular level is often called nutrient cycling. The movement of nutrients through the ecosystem is a continual process that includes the synthesis of body tissue in the living organism, the transfer of energy from one trophic level to another, and the release of nutrients from the body of an organism upon death and subsequent decomposition.

The whole organism participates in the redistribution of matter as it moves about, selecting a place to eat, rest, and perform its other daily activities. Some organisms move but a short distance during their entire lives, that is, they have a small home range. Others cover hundreds or even thousands of miles; many birds fly thousands of miles each year as they move from wintering grounds to nesting grounds and back to the wintering grounds. Some populations move as a unit. Herds of elk, mule deer, and caribou exhibit a seasonal pattern of movement or migration. Social interaction between individual animals within each herd adds an internal mobility to its external mobility.

The individual animal is the fundamental unit that must meet the energy cost of motion, or of life. The energy cost of life of each individual depends on its growth rate, reproductive condition, amount of daily movement, and other factors unique to that individual. Thus it is logical to analyze the energy relationships between an organism and its environment, determining the effect of different factors on the maintenance, growth, and reproduction of animals with different individual characteristics. How is this done within the basic framework of matter and energy? These two fundamental components of the ecosystem need to be regarded as factors and forces, with an understanding of their *effect* on an organism rather than a mere recognition of their association with an organism.

1-2 THE ROLE OF THE ANALYTICAL ECOLOGIST

The orderly progression of life processes in the natural world is the result of evolutionary development. The ecologist steps into this world and asks first, "What is present?" Natural historians have been doing this for many years, resulting in a very important body of knowledge describing the life histories and characteristics of organisms. Many of the responses of an organism, whether it is responding as an individual or as a member of a population, have been related to the presence of physical forces in its habitat, such as weather, food, space, and others.

The descriptive ecologist proceeds a bit further than the natural historian, relating observed characteristics of the organism to observed characteristics of the habitat in a quantitative way. This has resulted in the formulation of many ecological rules. Bergman's Rule is an example: animals living further north tend to be larger. These types of rules are generally applicable, although exceptions can be found in looking at detailed relationships.

The analytical ecologist asks the question, "Why?" He is interested in the mechanisms operating in the natural world. The recognition of simple relationships such as the condition of the range and the condition of the animal are pursued further by analyzing the requirements of the animal through time and the ability of the range to satisfy these requirements. Scientists working with domestic animals have been doing this for years, but these animals are subject to considerable control by man. Their genetic characteristics can be manipulated, their living space can be limited by fences or pens, their feeding regimen can be controlled and many other conditions can be imposed on them. The animal scientist searches for a combination of forces—feed, cover, and space—that will result in the attainment of a particular production goal. Thus, if a particular diet and feeding regimen results in the desired level of milk production, it may become a management recommendation if there are no other complicating factors.

The analytical ecologist who is concerned with free-ranging organisms does not have such straightforward production goals in mind. His interests lie in the natural world where he has little control. The animals attracting his attention are usually elusive, secretive creatures subject to natural rhythms in activity each day and each year. They feed in accordance with these natural rhythms rather than man's work schedule. Breeding follows from natural stimuli. Their lives are inexorably linked to the rhythmic and arrhythmic fluctuation in their relationships with other organisms, the range, and other natural forces. These natural characteristics present a challenge to the ecologist because he cannot make this natural world conform to his particular desires.

Domestic animals are not under the complete control of man, of course. They exhibit many natural rhythms and other characteristics that are continuations of their natural development. Animal scientists are becoming a bit more "ecological" in their thinking, especially after it has been realized that certain production limits cause complications in other aspects of the animal's biology. High-grain diets, for example, cause problems in the digestive physiology of dairy cattle.

Ecologists, however, can become much more knowledgeable in the field of animal biology if they avail themselves of the vast amount of information that has been accumulated about domestic animals. No animal violates the basic laws of matter and energy, and the literature on domestic animals contains many experimental analogs of natural events. Different diet levels, for example, are analogous to natural variations in the food supply. Different population densities in pastures, pens, or barns are analogous to natural variations in population densities.

The analytical ecologist needs to recognize the dynamic nature of the relationships between organism and environment in the natural world. He must be cognizant of the whole in addition to the relationships between its parts. He must always be ready to recognize the factors and forces that may be affecting an observed relationship. He must be able to establish the importance of different factors and forces present through time, which will enable him to predict the potential impact on the ecosystem that an alteration of these factors and forces would have.

1-3 DEAD OR ALIVE

Biologically, an organism may be classified as either dead or alive. If it is dead, it is subject to decomposition and the recycling of its nutrients through living systems in the future. This is a slow process, and the impact of a single organism on the nutrient cycling picture is usually not very great.

Ecologically, an organism is more than simply "dead or alive," however. If it is "not dead," then it is alive. There is a great possibility for variation in the ecological importance of each individual in the "not dead" or living category. An organism could be merely surviving, consuming resources sufficient only for existence, or it could be at its full productive potential—growing, reproducing, and contributing to population growth. Living organisms determine the growth potential of the population. The dead can contribute only as a part of the slow process of decomposition and nutrient recycling.

This book presents analyses of the factors that affect the living. Life in its fullest complexity cannot be comprehended by the human mind, but some considerations can be made that permit an understanding of some of the basic principles of life processes of organisms in their natural habitat.

1-4 PRODUCTIVITY OF THE INDIVIDUAL

The productivity of a living organism can vary from less than maintenance to maximum productivity as an individual, including both its body weight and size and its reproductive potential (Figure 1-1). An individual animal in a submaintenance condition may be experiencing a negative nitrogen balance with a subsequent loss of protein tissue; it may be in a negative energy balance as fat reserves

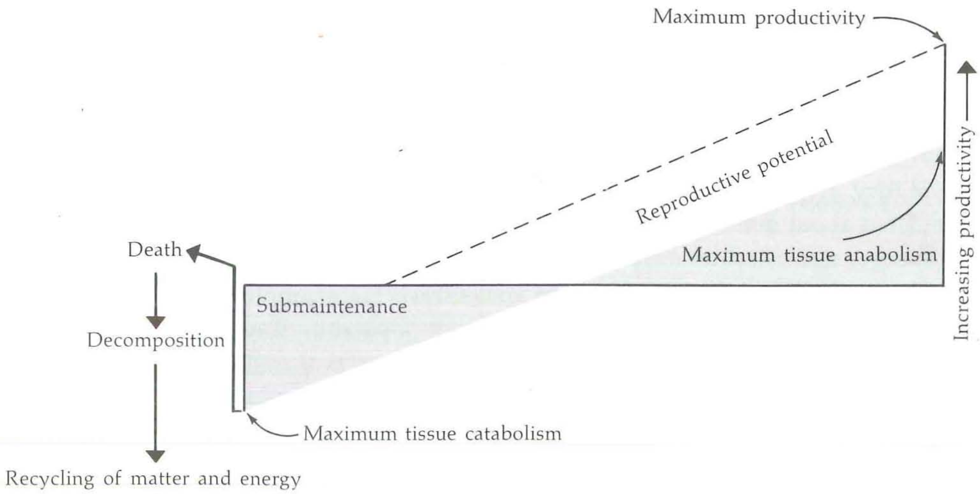

FIGURE 1-1. The productivity of a living organism can vary from less than maintenance to maximum productivity.

are being mobilized; and it may be losing vitamins, minerals, and water, which results in a general loss of body weight. Such overall patterns of weight changes are exhibited by all free-ranging animals. The general pattern for weight changes in wild ruminants shows clear variations in weight, with losses occurring in the winter in most members of a population, and in the summer also for lactating females.

Lactating females may be in negative productivity as an individual but positive productivity with respect to its suckling offspring. Several mammals exhibit weight losses during lactation, indicating that body reserves are being mobilized to produce milk that is of distinct importance for the survival of the offspring. Ecologically, then, an animal's productivity does not fall into a single category; it may be at two or more points simultaneously on the productivity scale shown in Figure 1-1. The ability of an animal to draw on its own reserves to enhance the survival capabilities of its offspring may be of particular ecological significance because every young animal that reaches reproductive maturity has the potential for contributing more animals to the population.

The young, immature, and rapidly growing animal is in a general state of positive productivity. Protein is being synthesized at a rapid rate, minerals are being deposited as the bones grow and ossify, and the total body mass is usually increasing. This continues beyond the point of reproductive maturity in most species, although there is usually a marked deceleration in the growth rate after an animal reaches reproductive maturity.

The reproductive potential of any animal has a genetic limit, but the actual rate of reproduction is less than that potential because of the effect of natural forces. It is important to consider the ecological potential for any reproductive process, including the production of different types of body tissue, eggs or fetal tissue, and the production of milk. The ability of an animal to cope with the demands of different biochemical processes is dependent not only on the rate of ingestion of nutrients at the time they are required, but also on its ability to translocate nutrients by the mobilization of reserves. Mobilization of protein material with the subsequent resynthesis of amino acids in fetal tissue is one example of translocation; another example is the reverse process, or resorption. Antler growth has been shown to result in the mobilization of phosphorus from the ribs. In deer, elk, and moose, the antlers are shed and the minerals enter a slow recycling process. This process begins when rodents eat the antlers, live, die, and decompose with subsequent resynthesis in plant tissue, once again becoming available to herbivores such as deer. Egg shells are produced by a similar process; some of the calcium deposited in the shell comes from food, and some from metabolic processes that result in bone deposition followed by mobilization for production.

The relationships between ingestion, metabolism, deposition, and the mobilization of nutrients indicate that time is a very important consideration in ecology. Organisms do not just live according to conditions at the moment, but their ability to cope with factors and forces impinging on them at a given moment is dependent on their previous life processes.

1-5 THE NATURAL MOSAIC

The challenge confronting the present student of ecology is that of integrating current information about the components of the ecosystem within a framework that utilizes technological capabilities for a systems analysis. The measurement of environmental parameters in isolation and the calculation of simple correlations between an environmental parameter and an organism's response is seldom, if ever, a meaningful educational experience by itself. Yet, certain general relationships have been described in the literature.

Many examples of parameters measured in isolation can be found in the ecological literature. Temperature has been suggested as a dominant ecological force, and, of course, there are both high and low atmospheric temperatures at which life ceases to exist. However, temperature is not the only changing parameter between, say, the equator and the North Pole. There is a northern limit for most species in the Northern Hemisphere, but other parameters must be taken into consideration. For example, vegetation changes are marked, culminating in the tundra with its unique vegetation forms.

High temperatures have been observed to cause a depression in the reproductive rate of domestic animals. Free-ranging animals can often avoid high-temperature areas, but heat stress can also develop because of excitement or increases in the metabolic rate caused by running. Thus high temperatures alone are not an indication of the potential for heat stress.

Wind has been considered an ecological force by many investigators. Meteorologists describe wind flow in terms of an average velocity over a vertical profile. Aerodynamic analysts consider laminar and turbulent flow characteristics. Ecologists talk of the responses of animals to windbreak effects. Some have reported that animals tend to bed in the areas with higher velocities; others report the opposite. Barometric pressure has also been related to animal behavior, and there are those who think animals can sense not only changes in pressure but also oncoming storms.

Relative humidity has been related to the responses of many organisms. In some cases there has been a positive response observed, in some, a negative one, and, frequently, no relationship is detected. Relative humidity is a function of barometric pressure, air temperature, and the vapor pressure of the air. The ecologist needs to be aware of the interaction between these components of energy and matter before a realistic appraisal of the relationship of an organism to moisture in the air can be made.

Precipitation is an ecological force that has been related to population fluctuations. Conflicting reports can be found in the literature on the success of pheasant hatching during periods of heavy rainfall. Some reports show a depression in the population during a wet spring, although others show an increase in the population. The amount of rainfall affects the eggs and chicks directly; it also affects the growth of vegetation and the insect population associated with this growth. Thus, the amount of rain, the type of rainfall, the timing of the rainfall, and other characteristics of this ecological force are necessary parts of a meaningful analysis that can be used to interpret an organism's responses, both as an individual and as a member of a population.

Snowfall has been given considerable attention by ecologists, since it functions as a mechanical barrier as well as a thermal barrier. Heavy snowfall may enhance the survival of a subnivean animal, since it is an excellent insulator. Snow increases the energy expenditure necessary for movement through it by an active animal, however. It also covers food; however, if it becomes encrusted, animals can walk on it and reach food that would otherwise be unavailable. Thus snow can have both detrimental and beneficial effects, and an analysis of the effect of snow must consider the function of the snow in relation to a given organism.

Light seems to be related to the daily and seasonal cycles of many animals. Some are nocturnal, such as racoon (although they are observed to be active during the day at times) and owls; others are primarily diurnal animals, such as game birds, song birds, and hawks; and still others are crepuscular, becoming most active in the transitional period between daylight and darkness. These differences in the timing of the activity periods of animals may result in almost total noninteraction of species even though they live in the same area. On the other hand, because activity patterns are not absolutely rigid, they may overlap. Thus the amount of interaction that can take place between different species occupying the same area can be represented by a gradient.

Seasonal reproductive cycles appear to have some relationship to the seasonal variations in length of daylight. Some birds are responsive to longer periods of daylight, coming into breeding condition in the spring and laying their eggs in the late spring and early summer. Breeding condition is reached earlier if artificial light is supplied. For example, the provision of artificial light in the pheasant yards at the Ithaca Game Farm on February 15 results in the first egg being laid on about March 10. Wild ruminants, with fairly long gestation periods, respond to shorter days and breeding condition is reached in the fall. Conception generally takes place between October and January, with births following in late spring or summer.

Daylength follows a regular pattern of change, but weather patterns are much more irregular. Spring weather may come much later in some years than in others, and this may delay forage production on the range so that it is not of sufficient quantity and quality to satisfy the requirements of animals after parturition. Effects of variations in weather, plant phenology, and other range conditions on animals are discussed in Part 6.

The thermal effects of radiation as an ecological force have been quite neglected. Livestock shelters have been designed to maximize heat loss to the clear cold sky in the summer. A "cloud" due to respiratory water loss may form above a herd of caribou, reducing the loss of infrared energy from the animals. This may result in little or no metabolic benefit to the animals since they may be moving at the time, causing their heat production to be higher. Thus, the effect of cloud cover, radiant energy, and other thermal forces cannot be determined without a larger analysis of the interaction between these forces and the rest of the animal's characteristics.

Soil type and fertility is an ecological force that permeates the entire food chain, affecting the selection of nesting sites, bedding sites, movement patterns, and the like. For example, deer have been observed to selectively graze on wheat that is growing on fertilized ground. The presence of pheasants seems to be associated with higher calcium levels in the soil. Selenium is a trace element in the soil that is necessary in very small amounts for metabolic processes and is toxic at higher levels. Both desirable and undesirable elements in the soil, along with a complex of other nutritive, physiological, and behavioral factors, affect the productivity of the individual animal. Thus the soil must be considered an integral part of a model that includes considerations of all the factors and forces present in the ecosystem.

Fire is an interesting ecological force. It is a part of the natural scheme of things, since lightning caused forest fires long before man entered the picture. These fires were naturally controlled if they took place in areas that had been burned previously and not enough litter had accumulated to result in a significant fire. Precipitation, which often follows lightning, was also a natural control. Fire causes immediate thermal effects because of high temperatures, and there is a sudden release of nutrients as the organic material is reduced to ash. These nutrients can then find their way into the nutritive processes of plants more quickly than decomposed material. On the other hand, fire can adversely affect the fertility of the soil by destroying organic binding agents in the soil, which results in a greater chance of erosion and an increase in the rate of leaching. Thus, the effects of fire are both short-term and long-term and should be considered to be a part of the whole ecosystem, since they interact with physical components, plants, and animals.

The chemical constituents of the soil are reflected in the chemical characteristics of the forage growing on it. Nutritive quality can be described in chemical terms alone, but this has little relevance in ecology since it is not what is present in the plants that is of importance, but what the animals extract and use from these plants. Thus net energy, rather than gross energy, is an indicator of forage quality. Similarly, it is net protein, rather than crude protein, that is of significance to the organism. Vitamins and minerals are necessary to provide a balanced diet, and the quantity of each that is needed from forage is determined by the requirements of the animals. Adult ruminants, for example, need no vitamin B because this vitamin is synthesized in the rumen. Monogastric animals, however, must rely on external sources for vitamin B. Some minerals act as metabolic inhibitors—selenium has already been mentioned—although some, including selenium, must be present in small but essential amounts. A lack of iron, for example, causes anemia, and this affects the metabolic efficiency of the body by depressing the ability of the blood to carry oxygen. Mercury has been found to affect the viability of pheasant embryos, although it seems to have little effect on the adult birds. Thus one needs to consider not only the mineral and its action in the metabolic machinery of the animal, but also the age of the animal at which this becomes a part of the organism-environment relationships. The time factor may be of real significance in the interaction between factors and forces that affect productivity.

1-6 INTERSPECIES INTERACTION

Several types of relationships can be found between different species in the natural system. Ruminants are dependent on the action of microflora and fauna in the rumen to break down fibrous forage material and produce organic chemicals (volatile fatty acids) that are a source of energy for the host. Heavy infestations of parasites may cause the host's death. Some parasites have a neurological effect on their hosts, causing aberrant behavior that renders the host incapable of coping with other environmental forces. Moose sickness (*Pneumostrongulus tenuis*) is an example of that type of effect. Pathogens may function in much the same way. Predators feed directly on prey species, and they also may affect the prey by harassment, by reducing their feeding time, or by causing other effects on behavior. Predator and prey may also coexist because of changes in the food habits of the predator owing to an abundance of alternate foods. Thus coyotes may feed heavily on fruits and berries, ignoring fawns that might have been a source of food if the berries were unavailable. The density of prey necessary to retain the interest of the predator is worthy of consideration; it is too easy to assume that predators are easily discouraged in the same manner that the human hunter is today. It is likely that the predator has much more at stake, and, consequently, has different thresholds for beginning and ending the utilization of a particular type of prey.

The variability in time and space that can occur in interspecific relations suggests that a comprehensive look must be taken at the entire interspecific community. Predation levels measured between two species alone simply cannot represent the effectiveness of predation in the natural world. Parasite numbers by themselves have little relevance in analytical ecology; it is an understanding of the mechanisms with which the parasite affects the host that is important for an interpretation of the meaning of the number relationship between parasite and host. How can an ecologist escape these basic and fundamental relationships?

1-7 INTRASPECIES INTERACTION

The interaction between members of the same species is frequently very strong, varying from open conflict to gregariousness. There are differences between species, of course, with some species, like the moose, being quite solitary animals that have little association with others of the same species. Other large ruminants, like the bison, are quite gregarious at almost all times of the year. The sociability of song birds, game birds, and waterfowl varies seasonally, with a general intolerance during the reproductive season, and gregariousness during migration, winter flocking, and the like. Some species have a distinct social structure at all times of the year, although the amount of gregariousness varies. The turkey is an example. Competition for food and space affects the amount of intraspecific tolerance; field mice (*Microtus*) in crowded conditions are much less tolerant of each other than when conditions are less crowded. The requirement for space by any species is a function of its basic requirements for matter and energy (food) and its reproductive condition and general behavior pattern at a particular time. Thus the living space required is a dynamic dimension that varies partly because of daily rhythms, partly because of seasonal rhythms, and partly because of local conditions at a particular time.

The areas of the home ranges of species in particular habitats are frequently calculated by ecologists. The size of the home range is dependent on the distribution of energy and matter within a space that the animal can traverse. There must be a maximum space over which an animal can roam and still ingest enough nutrients to supply the necessary energy for those movements. Animals move for many reasons besides foraging, including playing, breeding, escape, and other necessary activities that are a part of daily life. A smaller animal might have a higher requirement for energy and matter if it was a prey species that encountered predators frequently. Its home range might reflect that. Large animals require large areas for living space, and they may migrate seasonally to find sufficient space. Yet elk migrate to winter concentration areas that often do not provide enough forage to meet their current requirements, and the fat reserve is utilized in order to make up the energy deficit. Thus the significance of the home range and its characteristics extends through time; an extensive summer range may be of significant importance to survival on a restricted winter range. It is very important to consider these variations in space and time before the functional organism can be understood in relation to the distribution of energy and matter in its natural habitat.

1-8 REPRODUCTIVE PATTERNS

Reproductive patterns are often a reflection of seasonal variations in light or rainfall, or of the quality of the range, or of some other natural event. For example, the timing of the reproductive period of most birds is related to light, although waterfowl in some areas breed when rains are common and the water level is high. Lower reproductive rates are frequently observed on ranges with a lower soil fertility. Reproduction, however, is not a simple on-off process but can be represented by a gradient with a variable threshold at which breeding commences.

The significance of the number of reproductive attempts per year needs further consideration within a larger ecological model. One parturition may occur, as in deer. Smaller animals, such as *Microtus,* may have several reproductive periods per year. This is of greater interest than merely the number of young born in toto and in each litter. Young animals born at different times of the year enter different worlds: forage is changing, there are seasonal differences in weather, and the growth rate and subsequent productivity of these different litters is going to vary in part because of the different environmental conditions. The same effect may be observed in species of birds that renest if the first nest is destroyed. A successful second hatch after an initial failure may not be the same ecologically even if the same number of chicks are hatched. A late hatch has a different food supply owing to the phenology of the vegetation and insects, and there is less time for a late-born chick to grow and mature prior to the first winter. This may affect its ability to survive the winter and reproduce the following spring. The significance of these variations is of considerable interest to the population ecologist. This is especially true for an analytical ecologist who makes predictions based on organism-environment relationships rather than merely presenting a historical perspective based on large quantities of numbers.

The various relationships discussed in previous sections in this chapter include but a scattering of isolated examples among a large number reported in the literature. It is clear that ecological relationships are complex enough to demand a very systematic and organized approach to their analysis. It is also clear that these analyses must proceed within a comprehensive framework that includes at least the more important variables in the natural system.

The natural world is too complex to represent in its entirety. This text contains samples of analyses concerning the "principal characters" on the ecological stage, representing the main forces that are present, with suggestions of the effects of alternative responses that an animal might exhibit. The situations that are described are not all-inclusive, but the student is asked to consider the larger meaning of these analyses, relating the analysis under consideration to the larger whole. This might be called theoretical ecology, but perhaps a more appropriate term is "theatrical" ecology, with the written text containing profiles of the main characters in the ecological theatre, relating them to the rest of the characters in a compressed form in both space and time.

Just what or who are these principal characters? They are analogs of real organisms in the natural world. The scenes considered do not represent any one particular spot on earth, or any particular individual on earth; rather they represent an environment and an organism that could be present anywhere on earth. Thus the material that follows is not unique to only one situation at the exclusion of all others, but represents the factors and forces present in any ecosystem, with an indication of how these factors and forces might interact with specific organisms by the use of examples that illustrate mechanisms in operation.

1-9 A THEORETICAL MOSAIC

The analytical ecologist cannot present all forces and factors existing in the world. The alternative is to assemble an array of principal characters in the ecological theatre and relate one to another in a realistic manner with no more complexity than can be understood in each and every analysis. This results in an understanding of the role of different factors and forces in the real world, though the analysis may not be for any particular organism at a particular place at a particular time. The characters represent interactions, possible events, and dynamic relationships, making it easier to grasp the fundamental relationships displayed and apply them to particular areas of interest.

Theoretical considerations are hard to grasp conceptually, but they can be made less difficult by the use of specific examples. For example, topography is an ecological factor that affects the distribution of plants and animals, as well as physical components of the ecosystem such as water. We know from geometry that topographic variations reach limits contained within 360°. Practically speaking, topography varies from flat land to steep hills, which can be measured to find the flattest to steepest limits of topography. The analyst can then use a range of values between these limits to analyze the effect of topography on some other ecological factor.

The soil has particular water-holding characteristics. The limits are clear though; the soil may hold none of the water that reaches it, or it may hold all of the water that reaches it. The actual amount retained by the soil is a function of gravity, soil particle size, slope of the substrate, and characteristics of the soil profile. Interactions between water and soil may be reduced in simplest form to specific interactions such as surface runoff, percolation, or some other analysis that considers a minimum of factors. When the simple analysis is understood, additional factors are added to approach greater and greater ecological realism.

Vegetation can be represented theoretically by considering limits to its distribution. There is an upper limit to the growth of trees, which is a function of genetic potential and physical forces such as gravity, wind, and so forth. There is a horizontal limit to the spread of branches; they cannot extend further than the mechanical structure of the woody tissue will support. Thus the principal features of vegetation can be placed within limits that have very fundamental relationships to basic natural laws. If these are recognized as the outer limits, then the effect of additional factors and forces can be added that will indicate why these maximum physical limits are not reached. Such things as life form, strength, mechanical density, optical density, and energy and matter distribution can all be considered and are discussed later in this text.

Weather patterns vary daily in a given locality and are different between different localities. The complexity of wind, cloud density, and other characteristics of the atmosphere is great, but again there are limits that can be recognized for each of those weather parameters. Atmospheric interference reduces the solar radiation striking the earth's surface. Cloud density can be treated as a variable between a minimum of zero—as in a clear sky—and a higher density limit that represents maximum cloud cover such as heavy fog at ground surface. Thus a principal weather character called solar radiation can be described in terms of maximums and minimums that are dependent in part on atmospheric conditions. Thermal radiation can also be treated in a similar way, as can wind, vapor pressure, and temperature. Their patterns are somewhat regular and in each case can be represented by theoretical or observed limits, permitting one to test the ecological effect of variation in each by using a range of values for each parameter within the limits established.

Organisms themselves are principal characters in the ecological theatre, but the analytical ecologist cannot handle all of them in a beginning analysis. Theatrical productions frequently contain a small number of actors and actresses, each of whom represents something larger than himself. Analytical ecology is best approached by using actors too. Each deer considered represents more than an individual animal of a given species; of greater concern is its relationship to the factors and forces in this ecological theatre. It should be related to the forces of topography, water, weather, and food, with an understanding of how it relates to these forces in a simple way before the plot becomes more complex. Further, if fundamental characteristics are considered, the same approach and the same principles apply to any organism that might be considered, permitting an ecologist to apply the principles in his own particular area of interest.

Once the role of a single principal character is understood, two characters might be considered. These could be members of the same species—a doe and a fawn could be related analytically—or they could be of different species. A deer and a wolf, for example, could be considered together with an analysis of their chances for contact, energy flow, energetic efficiencies, or a host of other fundamental considerations. In this situation, the deer represents primary consumers, or animals that feed primarily on vegetation. The wolf represents secondary consumers, or animals that feed on other animals. The basic characteristics of energy and matter are applicable to all species, and the progression of the analysis from the simple to the complex may proceed from consideration of a single animal to two, four, and then larger populations, to communities, and finally to the entire ecological organization.

A frequent approach in ecology has been from the entire ecological organization first, but this presents many difficulties because the dynamic relationships between an organism and its environment are lost in the complexity of the total picture. The result is that students have learned only generalities, "rules," and similar sorts of conclusions that are devoid of the drama associated with the life of the individual. Yet each organism lives or dies as an individual, and its productivity is uniquely its own—a function of the effects of the independent, the compensating, and the additive ecological forces present in its environment. Students will find it exciting to build these analyses from the component parts (the principal characters that they choose), working from the simple "one-act play" to the complex *n*-dimensional analysis of populations, communities, and systems. The phrase "building the ecological model from the inside out" illustrates the reverse approach taken.

IDEAS FOR CONSIDERATION

Can you grasp the idea of differences between knowledge in empirical, factual form and an understanding of the role of energy and matter, in the form of individual organisms in a dynamic ecosystem?

Eggs and milk are different forms of matter. Ecologically, however, their functions are similar. Both require a female's metabolic activity for synthesis, and both are a part of the perpetuation of a species. What other functions can you identify that are taxonomically different but ecologically similar?

What limits can you describe for various components of the ecosystem? Can you identify the maximum and minimum due to physical laws, and then identify more realistic ecological limits?

What basic, functional similarities do you find between plants and animals? What basic differences are there, in terms of energy and matter utilization and synthesis? How different are primary consumers (herbivores) and secondary consumers (carnivores)? Are these differences more characteristic of variation in habit rather than of basic functions? What about their roles in energy flow? Are you prepared to recognize the role of each as an individual and yet relate each to a position on a trophic level?

Why not assemble life-history data for species of direct interest to you to become acquainted with their "personalities and life styles"? Rather than being simply the extent of your knowledge of them, this information can be used in later analyses.