2

INTERACTIONS BETWEEN ORGANISMS AND ENVIRONMENT

2-1 FUNCTIONAL RELATIONSHIPS

An understanding of the relationships between an organism and its environment can be attained only when the environmental factors that can be experienced by the organism are considered. This is difficult because it is first necessary for the ecologist to have some knowledge of the neurological and physiological detection abilities of the organism. Sound, for example, should be measured with an instrument that responds to sound energy in the same way that the organism being studied does. Snow depths should be measured in a manner that reflects their effect on the animal. If six inches of snow has no more effect on an animal than three inches, a distinction between the two depths is meaningless. Six inches is not twice three inches in terms of its effect on the animal!

Lower animals differ from man in their response to environmental stimuli. Color vision, for example, is characteristic of man, monkeys, apes, most birds, some domesticated animals, squirrels, and, undoubtedly, others. Deer and other wild ungulates probably detect only shades of grey. Until definite data are obtained on the nature of color vision in an animal, any measurement based on color distinctions could be misleading.

Infrared energy given off by any object warmer than absolute zero ($-273\,^{\circ}C$) is detected by thermal receptors on some animals. Ticks are sensitive to infrared radiation, and pit vipers detect warm prey with thermal receptors located on the anterior dorsal portion of the skull. Man can detect different levels of infrared radiation with receptors on the skin, but they are not directional nor are they as sensitive as those of ticks and vipers. Thus we must conclude that the environment of lower animals is probably very much different from that of man and is dependent on their own capabilities for detection of environmental stimuli.

This leads to a very basic question: What are the neurological and physiological capabilities of an animal for detecting environmental factors? Can it see? What wavelengths can it distinguish, or is it seeing only varying shades of grey? What is its hearing range? Does the range change with age? What odors can it detect? What are the minimum or threshold levels necessary before detection of a stimulus can occur? What stimuli are not detected neurologically, but affect the animal physiologically?

There is a dearth of information on the sensory and physiological characteristics of wild species. Burton (1970) has published a general summary of the literature on animal senses, including references to several of the more refined sensory capabilities of some species. Information on the more common larger animals of North America is virtually nonexistent. We can conclude from field observation that deer, for example, do have a more sensitive sense of smell than do humans, and they seem to hear better too. Technical capabilities available to the researcher today make it possible to go beyond this superficial level of knowledge of the sensory capabilities of an organism, however. Sensors are available for the measurement of a multiple of physical and chemical environmental characteristics. The value of such sensors depends on how closely the measurement approximates the detection capabilities of the organism being studied.

Techniques are also available for the study of the physiological characteristics of free-ranging species. What are the heart rates of free-ranging animals? What are the red blood cell counts, and how do they vary diurnally? What relationship exists between the number of red blood cells and the ability of the blood to supply oxygen to body tissues? What is the relationship between the heart rate, red and white blood cell counts, oxygen consumption, and the animal's ability to withstand infection by parasites, endure cold weather, escape when pursued by a predator, or cope with other environmental forces?

Consider nuclear radiation, an environmental component that is detected physiologically but not neurally. What dosage can the animal withstand before death occurs, and what is a lethal dose for 50% of the population? What effect does a sublethal dose have on the reproductive capacity of the individual or of a whole population? on its ability to survive predation? What effects do herbicides and other organic poisons have on the survival and production of nontarget species? Do they affect the survival of the individual? suppress reproduction? or both? Do they affect the social hierarchy and territorial behavior of wild animals, thus reducing reproduction even without a change in the physiological condition of an animal?

These are important ecological questions. The effect of organism-environment relationships is not merely one of life or death, but variability in the organism's response to environmental forces. The effect of this variability is reflected in productivity, and variation in productivity results in differences in population levels and the distribution of energy and matter in the entire ecosystem. The excitement of an analytical approach to the study of ecology lies in beginning

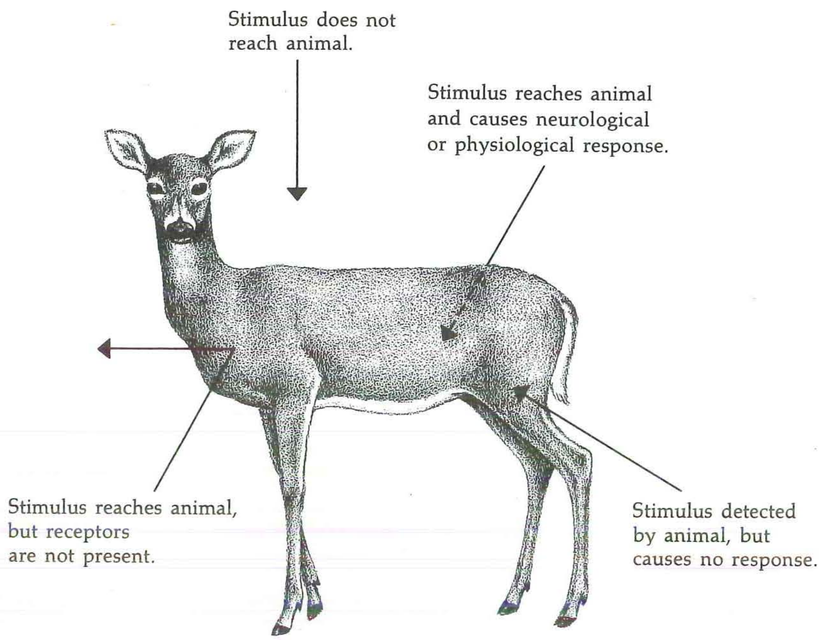


FIGURE 2-1. The environment of an animal is limited to the energy and matter that has a neurological or physiological effect on it.

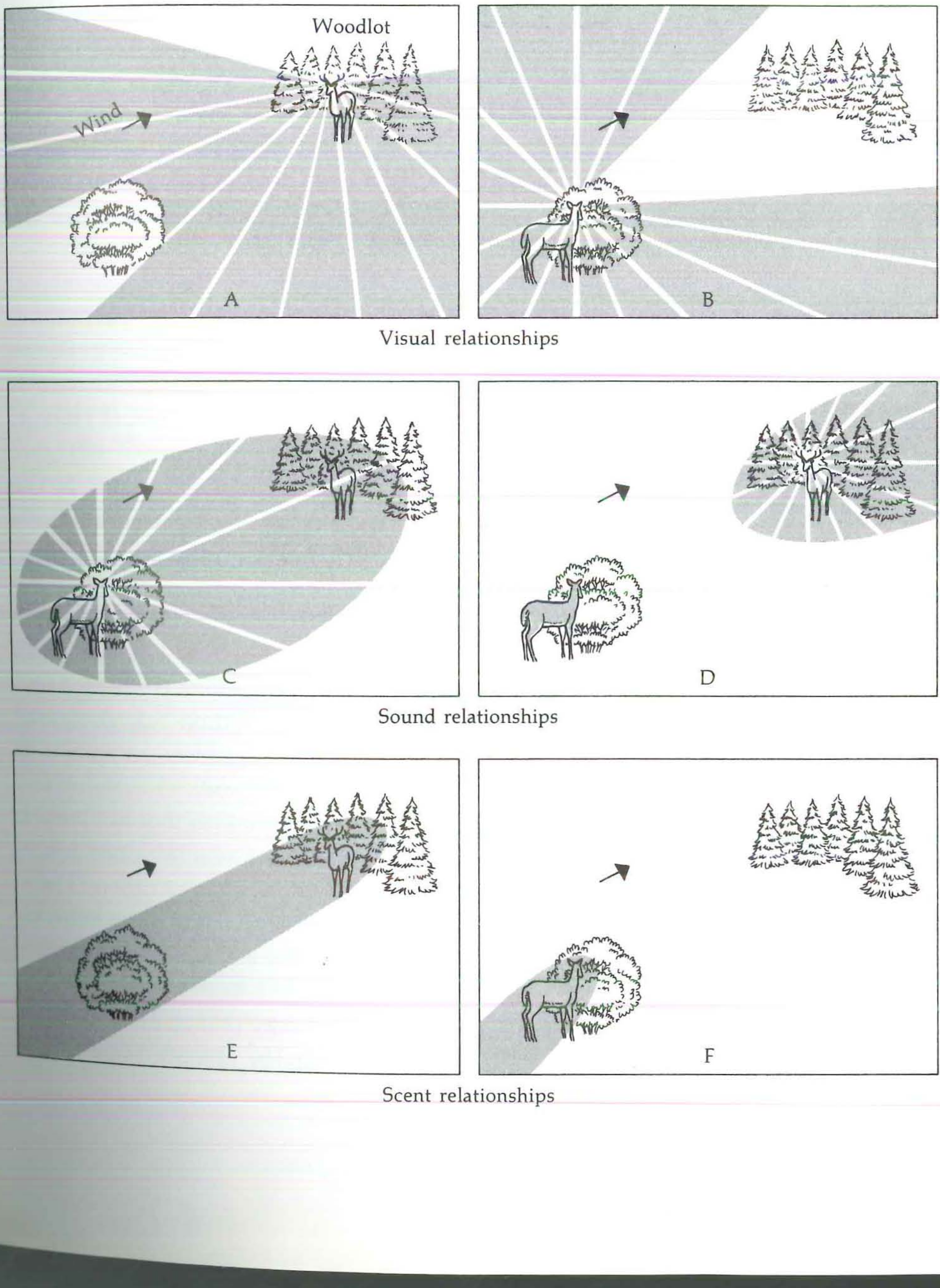
to understand how these things relate rather than in merely seeing the effects of all these interrelationships buried in a mass of numbers representing the presence of *n* number of organisms in a particular place.

Meaningful relationships between organism and environment exist only when a stimulus reaches the organism and has either a neurological or a physiological effect on it. Environmental forces or stimuli that do not reach the organism or are not detected by it cannot be considered part of a *functional* organism-environment relationship. All possible organism-environment relationships fall within four groups (Figure 2-1):

1. Stimulus does not reach the organism. There is no functional relationship.
2. Stimulus reaches the organism but is not detected. Again there is no functional relationship.
3. Stimulus reaches the organism and is detected by the organism, but causes no response aside from detection. This relationship is of little importance to either the organism or the ecologist.
4. Stimulus reaches the organism, is detected neurologically or physiologically, and the organism responds to the stimulus. This is the kind of relationship that the ecologist must consider.

It must be recognized that there are differences in the type and amount of stimuli received by any two organisms at a given point in time, simply because no two organisms can occupy the same space at the same time. Further, no two organisms will have identical neurological or physiological thresholds at which stimuli are detected and responses made. The individuality of the relationships between an animal and its environment is illustrated in Figure 2-2. Certain conditions exist in the environment: the wind blows from a certain direction, locations of trees are plotted, and thresholds for detection of stimuli are assumed. Note in Figure 2-2A that the visual relationships are dependent on the location of objects in the habitat. If the woodlot located to the right of the animal is so dense that it is essentially an opaque wall, the visual relationship will extend up to it and no further. To the left of the animal, vision is limited by a single shrub

FIGURE 2-2. The environment of each animal is different, depending on its own receptor capabilities and on the distribution of energy and matter in the environment.



at certain angles but extends for greater distances where there are no obstructions, as indicated by the dots following the lines of sight (— . . .). The shape of the visual environment in Figure 2-2B is quite different from that in Figure 2-2A. Note that the animal in each of the diagrams would be visually excluded from the other. The indicated wind direction has no effect on these visual relationships.

The patterns of the sound relationships in the environment are considerably different from the patterns of visual relationships (Figure 2-2C). Sound penetrates the woodlot, and the shape of the ellipse representing the sound relationships in 2-2C is partially dependent on the direction of the wind, as sound energy travels slightly further downwind than upwind. If the wind is blowing strongly, the noise of the rustling leaves on the trees will be louder than many other sounds. Thus on a still day the sound pattern for an animal in a given place is more circular and larger in size than on a windy day, assuming that the loudness of the sound is similar in both instances. Note that the animal in Figure 2-2C can detect an animal next to the shrub, but the reverse is not true in Figure 2-2D.

The scent relationships in the environment have a shape that is highly dependent on wind direction (Figure 2-2E). Objects that can be smelled are detected at quite a distance if the source of the odor is downwind. The actual distance depends on the concentration of the detected molecules. This is a function of the strength of the source of the odor and of the velocity and turbulence of the wind.

A comparison of the patterns of the scent component in the environmental relationships in Figure 2-2E and F indicates the effect of wind on the distribution of scent molecules. The animal in Figure 2-2E could detect the animal in Figure 2-2F, but the latter could not detect the former. If the wind were to switch directions, however, a reversal in the pattern of scent relationships would emerge. The animal in Figure 2-2F could detect the one in the position shown in Figure 2-2E, but the reverse would not be true. Thus the scent relationships in the environments of these animals would change without any change in the animal's physiology or behavior.

Analysis of the response of an animal to taste is difficult because of the subjective nature of the response. A common approach is to record the responses to a variety of chemicals. This was done for black-tailed deer; they were presented with salty, sour, sweet, and bitter compounds in water solutions (Crawford and Church, 1971). Their consumption of the experimental solution was compared with their consumption of tap water. These deer, whose ages ranged from 5 to 14 months, showed preferences for some salty solutions (sodium acetate), but not for NaCl. They showed a preference for acetic acid solutions, but not butyric or HCl solutions. Strong preferences were demonstrated for sweet solutions. Males and females responded differently to bitter solutions, but not to the others. These preferential responses, not only between types of taste sensations but between different compound solutions within a single type, demonstrates the complex nature of the taste response.

The sense of taste in birds has been reviewed by Welty (1962). He concludes that it is poorly developed, pointing out that the number of taste buds is low and that they are distributed at the sides and base of the tongue rather than at the tip.

The various senses are all participating in the process of communication between an organism and its environment. Some environmental stimuli are not detected by the senses, but have an effect on physiological processes. Nuclear radiation is an example; the effect of radiation is not "felt" neurologically, but the physiological functions of certain tissues may be effected.

These examples illustrate that *it is the neurological and physiological capabilities of the organism itself that link it to its environment.* It is necessary to think of the environment in terms of its functional relationship to the organism rather than merely as the physical or geographical area in which it lives, if the dynamic relationships between an organism and its environment are to be understood.

The necessity for consideration of the conceptual basis upon which ecologists analyze organism-environment relationships has been heightened by the rapid increase in the capabilities for studying free-ranging animals by radio telemetry techniques. No longer must the field biologist rely only on visual observation of an animal, or on indirect observation of animal activity by tracks, pellets, or other signs. The location of an animal and information about its activity and physiology can be transmitted continuously from the animal to a receiving station.

2-2 THE SCOPE OF THE ENVIRONMENT

OPERATIONAL, POTENTIAL, AND HISTORICAL RELATIONSHIPS. In order to understand what causes an animal to "do" something in a behavioral, psychological, or physiological sense, it is necessary to recognize the stimuli that are in operation at a given time (Mason and Langenheim 1957). If we require only that a stimulus have an effect on the organism, the examples of stimuli that cause the responses given earlier in this chapter fall into the *operational* category, and the habitat components that are not detected by the animal or that do not influence his behavior or physiology in any way are naturally excluded from the environmental relationships. The removal of these habitat components will have no effect on the organism, and the propagation or perpetuation of these nonoperational features is wasted effort.

In addition to the operational components of the environment, there are habitat components that *could become* operational and those that *have been* operational. The former can be called *potential* and the latter *historical* environmental relationships. Thus the very important dimension of time is included in the potential and historical categories, and the various stimuli that elicit a response are recognized at a given point in time.

Several examples of the potential, operational, and historical relationships will illustrate the logic of these categories. Suppose that a deer was standing in an open field exposed to a strong wind on a cold winter day. If a shrub was located 50 yards away from the animal and at right angles to the wind direction, the shrub would not have an effect on the thermal balance of the deer (Figure 2-3A). The deer, however, has the ability to traverse the 50 yards and use the shrub

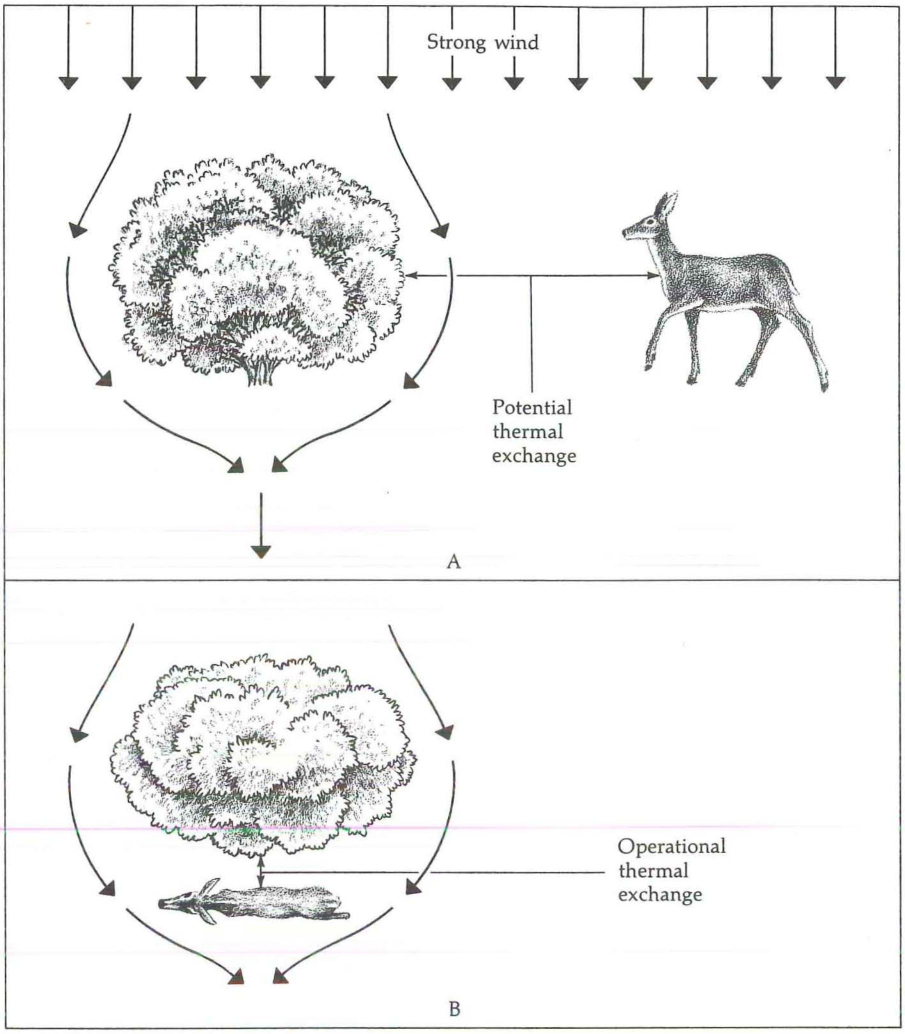


FIGURE 2-3. The potential and operational characteristics of a shrub in the environment of a deer with respect to thermal exchange.

for protection from the wind. As long as the deer is some distance from the shrub, the shrub can only have a potential effect with respect to air flow and thermal exchange. If the deer moves behind the shrub, placing itself in a more favorable thermal-exchange situation, the shrub is no longer in a potential relationship with the deer but is operational (Figure 2-3B).

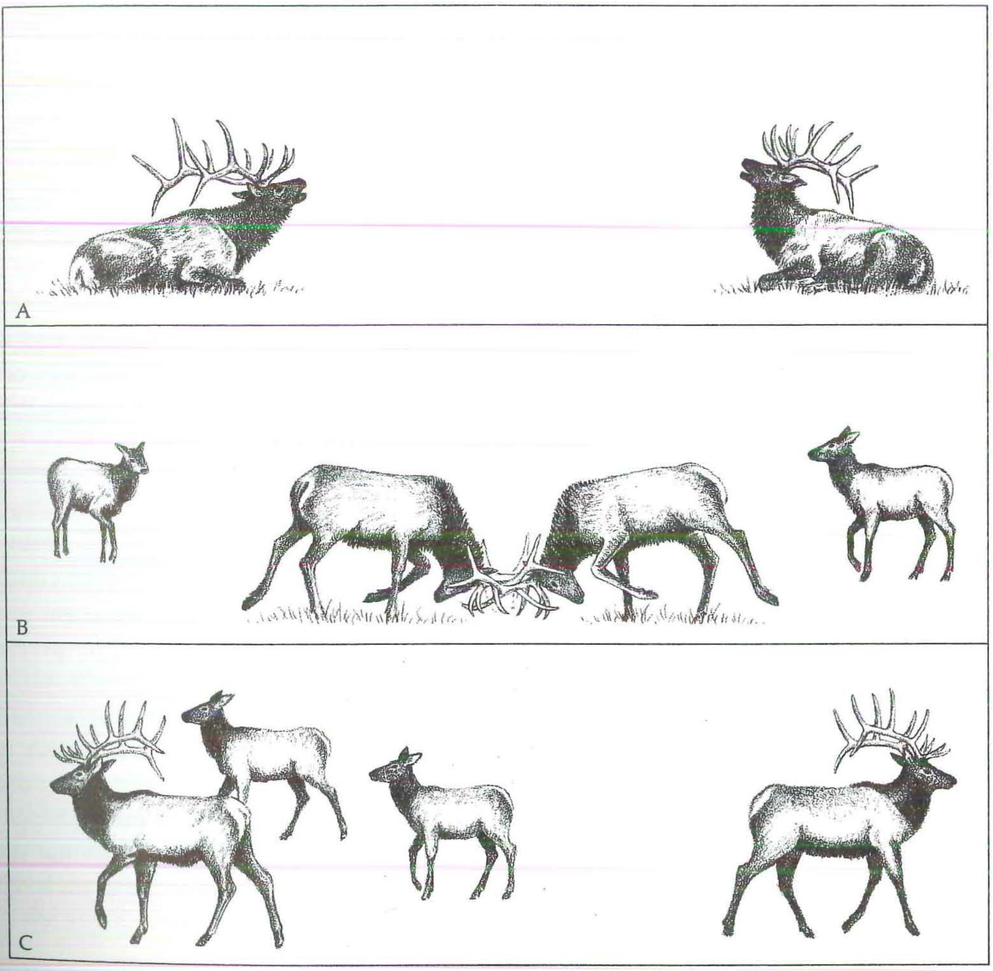
Or suppose a male elk has bedded down during the rut, and another male elk is bugling at a distance too great for the sound to be detected. The bugling male elk has only a potential relationship with the resting male; as far as the latter is concerned, the challenger does not even exist (Figure 2-4A).

If the bugling elk moves close enough so the sound can reach the second elk, the latter may, if he is in breeding condition, respond to the challenge. The sound of bugling then takes on a definite operational characteristic (Figure 2-4B). The subdominant elk, determined by the comparative aggressive behavior of the two bulls, then has an encounter in his memory that is a historical relationship; he does not challenge the other bull for the dominant position and control over the harem (Figure 2-4C).

There is a wide range of results that might be produced by the operational relationships between an animal and its environment described in the preceding paragraphs. Movement of a deer to the lee side of a shrub may have little or no effect on the thermal balance of the deer, or it could be critical to the maintenance of homeothermy. The resting male elk may pay little or no attention to the other male, or he may respond very emphatically if in the proper breeding condition.

Aside from genetically determined instinctive behavior that is not dependent on a learning experience by the animal, the historical relationships develop only

FIGURE 2-4. The (A) potential, (B) operational, and (C) historical characteristics of the environmental relationships between two male elk.



after operational relationships have occurred. At some time in the past, the deer may have experienced a reduction in heat loss when it moved to the lee side of a shrub. That same deer may then "recognize" the effectiveness of the shrub in reducing the velocity of the wind passing its body and could place itself again in the more beneficial situation. This requires some sort of a memory; the animal must have the capacity to be conditioned by a characteristic of the environment before there can be a "history."

The potential-operational-historical series becomes complicated very rapidly for living organisms. When the deer first sees the shrub, the shrub has an operational *visual* relationship with the deer as light waves are received by the retina and are interpreted by the brain. Until the deer moves to the protection of the shrub, however, it has only a potential *thermal* relationship. Thus an object in the environment can have an operational relationship for one type of stimulus-response combination and a potential relationship for another.

The behavior of the resting male elk will depend on its breeding condition. Whether the call of one male elk elicits a strong response in another depends on the hormone balance at that particular time. This is an internal thing, suggesting that in addition to an external environment there is an internal environment that includes stimuli that illicit a response. The role of hormones in determining an animal's response is an important part of the total animal-environment relationship. The ecologist must recognize these internal relationships in order to explain a large number of responses that are observed in the field. The hormone balance may be affected by external influences, such as light. Thus breeding activity might be described in terms of a day-length, hormone-balance, breeding sequence, with physical, physiological, and behavioral factors operating.

TIME. The idea of time is very simple in a physical sense because of the regular pattern of spatial relationships between the sun and the earth that results in a calendar year and regular periods of day and night. The concept of biological time is considerably more complex. A biological definition of time might simply be that it is "a measure of the intensity of life." Thus hibernating animals may spend four or five months of the year in a very passive condition, and the metabolic requirements over the entire period of hibernation may be equivalent to only a few days of intensive living during the active period of the year. The existence of diurnal and seasonal variations in the physiological condition of an animal indicates that chronological time is inadequate to represent physiological or behavioral events because the organism is not regulated as precisely as the rotation and revolution of the earth.

The age of an animal is another factor affecting its sensory capabilities. The environmental relationships of the developing fetus in the uterus are mostly chemical, and the fetus responds physiologically to the components of its limited environment. Two of the most important processes include the exchange of oxygen and carbon dioxide and the transfer of nutrients across placental membranes. Neurological detection mechanisms of the fetus are quite undeveloped and some—for example, sight—are quite unnecessary.

At birth, the young animal is suddenly exposed to vastly different environmental relationships. Senses are needed, but some neurological capabilities may remain undeveloped for days and even weeks, such as sight in members of the cat family. The newborn bobcat lives in a world filled with scents, sounds, and the touch of physical objects and litter-mates, with no visual relationships for several days. Members of the deer family, on the other hand, are alert and active within a few hours after birth.

As the animal matures, its senses develop and along with them, historical relationships. Thus the old buck thoroughly familiar with its home range is less susceptible to mortality than the newborn fawn. An animal in its prime of life, with maximum neurological and physiological development, has the most complex environmental relationships that it will ever have.

As an animal grows older, the aging process produces a general loss of sensitivity and elasticity of body tissue. Thus hearing is reduced, eyesight becomes weaker, muscular tissue is less capable of sustained contraction, and bones are more brittle. As these changes take place, the capabilities for the detection of stimuli are reduced, along with the animal's ability to react to them. The animal is more subject to predation, mechanical injuries, and other decimating events. The physiological effects of certain environmental components are frequently more severe in an older animal. DDT, for example, accumulates in body tissue and may reach a critical level as the animal grows older.

In summary, the complexity of the environmental relationships depends on the complexity of the nervous system and physiological characteristics of the animal. This does not mean that more complex animals have a greater ability to detect each and every stimulus; man has sensory abilities significantly inferior to those of many lower animals. The total overall complexity of man's environmental relationships is greater because of a highly coordinated nervous system.

ASSOCIATED RELATIONSHIPS. It has been stated that each individual organism has a unique relationship with its environment at any point in time. This environment includes potential, operational, and historical components. The organism does not live by itself in an ecological vacuum, however, since there are many other organisms with their own specific environmental relationships that are associated with and necessary for its survival. Bacteria functioning as decomposers, for example, may not be detected neurologically by humans. They cannot be seen without magnification, yet they are essential for converting organic material to simpler organic substances and inorganic compounds that are cycled through the ecosystem. The end product of decomposition processes (humus) is detectable, and life as we know it on this planet would be impossible without these bacteria.

Consider also the rumen microorganisms in ruminants. The host animal is neurologically unaware of their presence. The microorganisms have no direct physiological link with the host animal, but they are essential to the host who is dependent on the end products of their metabolism. The host even derives some amino acids from their dead bodies as the microorganisms themselves are digested in the small intestine.

Thus there is an ecological complex of environmental relationships, or associations of organism-environment relationships that may be independent, dependent, compensatory, additive, symbiotic, or in some way related. In simple terms, the environment of any organism includes other members of the biota and the functions of these associated relationships are of ecological significance.

HABITAT EVALUATION. A distinction should be made between habitat and environment. The environment has been discussed as a functional thing, something that relates to the organism under consideration. It can only be described in terms of the organism and includes the things that the organism can experience. The habitat, on the other hand, is simply the place in which an organism lives. It is the physical area inhabited by an organism and, on a larger scale, by the species. Thus we can talk about pheasant habitat, deer habitat, wolf habitat, and so forth, simply because those animals live there.

The habitat of an organism includes the organism-environment relationships of all species present there. Thus an area can be both pheasant habitat and fox habitat at the same time, but the environments of these two species are quite different. Indeed, the environments of two individuals of the same species are different.

An evaluation of habitat requires the recognition of those things that relate to the organism under consideration. What is present that the organism responds to? What kinds of responses are made? Does the environmental factor increase productivity? decrease productivity? Does it affect overt behavior? Does it affect some subtle physiological characteristic? Let us examine several characteristics of a habitat and consider how they might relate to the environment of an organism.

Optical density is a measure of the penetration of light through cover. There are absolute limits to this penetration, depending on the degree of transparency or opacity of the material. Vegetative cover ranges between complete transparency (no overhead cover present) and complete visual opaqueness. There is vertical density (Figure 2-5), which can be described in terms of the percentage of the sky that is visible directly overhead. At angles less than 90°, there is a decrease in the transparency and the optical density may reach a maximum even in cover that is quite sparse. This "venetian blind" effect is of interest both optically and thermally.

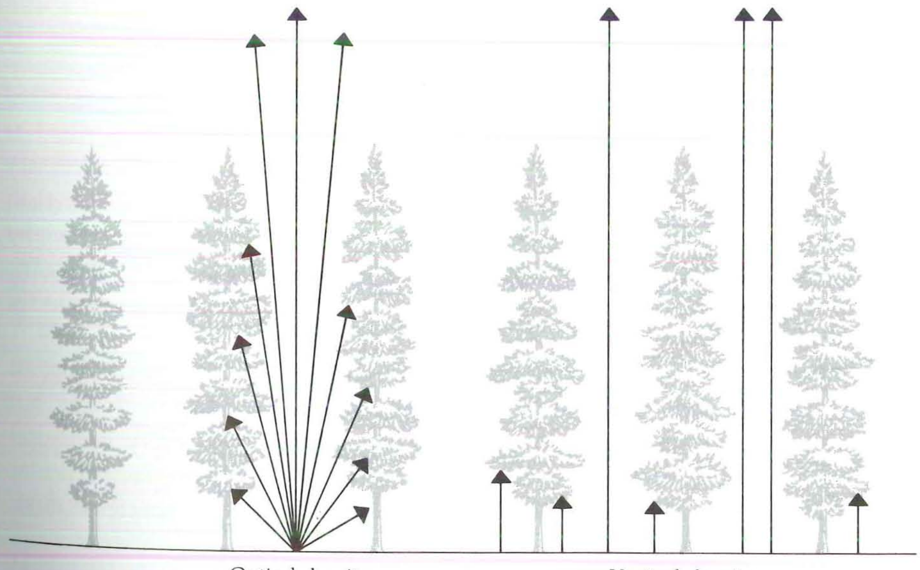
How does the optical density relate to an animal living in that vegetative cover? If the animal is subject to predators that hunt by sight, then optical density is of particular importance. Optical density is significant to both predator and prey, however, and what the predator can see and what the prey can see are equally important in an analysis of predator-prey relationships. The significance of these visual characteristics is dependent on the escape mechanisms of the prey. If an animal relies on the sighting of a predator as a stimulus for escape behavior, complete transparency might be the best cover for this particular relationship. Some species of ducks, for example, select nest sites in very open places, and may depend on their ability to see to warn them of the presence of predators.

Deer frequently bed down on or near the tops of hills, permitting them to see for some distance. They also bed frequently in small thickets, and this may be advantageous because it is much easier to see out from thickets than it is to see an animal in a thicket, especially if its color blends in well too.

The *mechanical density* of cover can be described in terms of the percent volume occupied by mass of a particular type, but this information is meaningless without an identification of the size and mobility of the organism that might be using the cover. Viruses can go through extremely small holes, penetrating material that appears to be opaque and solid to the human eye. Pheasants can travel easily through the lower few inches of vegetation. Deer can travel through brush that stops many a hunter, even though they may weigh about the same (say, 150 pounds). This brings to mind the importance of posture. A deer walking on all four limbs has a different posture than an upright man, and the difference in the distribution of the weight on the deer skeleton permits it to be much more mobile in dense brush. This clearly indicates that mechanical density can be described in a meaningful way only when the characteristics of the organism are also described.

Thermal density has characteristics in common with optical density. The downward flux of radiation from a plant canopy is less from the zenith than from angles less than 90° when the sky is clear. If the sky is cloudy, the environment of an organism is thermally uniform, and the thermal-density effect of vegetative cover is masked by the thermal-density effect of the cloud cover. This indicates that the description of a habitat characteristic may be dependent on the presence or absence of another habitat characteristic with which it may interact. This is true

FIGURE 2-5. The optical and vertical density of vegetative cover.



for solar and infrared interaction with reference to thermal density too; physical and biological materials have different reflection, transmission, and absorption coefficients for different wavelengths, and these affect the interaction between organism and environment. This is discussed further in Chapters 6 and 13.

The taxonomic structure of a plant community has often been used to describe that community. Thus species lists, abundance lists, frequency distributions, and the like have been used to characterize a plant community. This may be adequate from a humanistic, systematic point of view, but what about the other organisms living in that community? If two plant species have the same chemical characteristics that provide the same nutritive value to an animal, then these two different species are really the same in the nutritive relationships for the animal in question. Perhaps the life form of two different species is very much the same—different maples, for example, look very much alike in general life form—and the optical density, mechanical density, or some other factor that is experienced by an animal may indicate no difference between the different species. In that case, the environment of the animal is much simpler than the taxonomist might make it. Similar plant species may provide the same kind of mechanical support for nest sites. In that case the separation of species would be superfluous. This is discussed further in Chapter 15.

Consider also the source—internal or external—of stimuli that elicit responses from organisms. It may be difficult to separate internal from external stimuli. If a parasite is in the mouth of an animal, it is internal when the mouth is closed and external when the mouth is open. Or consider the intestinal parasite—it really is on a surface continuous with the outside of the animal; and although it might be inside something, it is not in a closed anatomical position, as is a blood parasite. Then too, it is possible for the organ systems to be closed to some organisms, but open to others. Viruses, for example, pass through cell membranes that are impervious to larger organisms, just as a deer exclosure may be closed to deer but open to snowshoe hares.

The role of any organism or species in an ecosystem cannot be categorized in simple terms with respect to other organisms, but can only be described as a functional part of different ecological processes. This philosophy is necessary for the analytical ecologist who recognizes ecological relationships rather than the mere presence of organisms in a natural environment. It is a unique philosophy that at times ignores taxonomic lines, and at other times it may further define the role of particular members of a species as interactions between other species are recognized.

Similarities in function between different species of plants or animals suggest the idea of "ecological equivalents." Taxonomically they might be different, but ecologically they might be similar. This is not true for their every ecological function, however. Different species are ecological equivalents only for particular functions, and it is necessary to think of individual organisms and species as fluid, labile entities that function in different ways in time and space.

The next chapter includes a discussion of the use of models in ecological analyses. It is a simple introduction to model building, with more detail included in the various models that follow in later chapters. The important point to remember is that the simple models are centered on the organism in relation to the environment in a functional way.

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IDEAS FOR CONSIDERATION

The following books and articles contain information about the relationships between organisms and their environments. Evaluate the data in these papers, assembling some thoughts and examples of specific organism-environment interactions based on the strength of the stimuli and the responses of the organisms.

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