6

WEATHER AND THE PROCESSES
OF THERMAL
EXCHANGE

Weather has long been an important consideration of ecologists. It is important
for the analytical ecologist to remember that he is interested in the *effects* of weather
on organisms. An analysis of functional relationships between weather and
organism causes the analytical ecologist to consider the distribution of thermal
energy, since it is thermal energy that is the most common bond in these rela-
tionships. Analyses of thermal energy relationships between an organism and its
environment are centered on the four basic modes of heat transfer. These occur
within the organism, in the interface between the organism and its environment
(a thermal boundary layer), and between the environment and the thermal surface
of an organism. All organisms are continually exchanging thermal or heat energy
with their environments by these four modes. The rates of thermal energy ex-
change depend on the thermal characteristics of the organism and its environment
and the interaction between different modes of heat transfer between the two.

6-1 THE FOUR MODES OF HEAT TRANSFER

Thermal energy is exchanged between animal and environment by radiation,
conduction, convection, and evaporation. A conceptual picture of the complex
nature of heat exchange for a free-ranging animal is useful for recognizing com-
ponents of the energy regime (Figure 6-1). It is impossible to describe mathe-
matically all of the dynamic thermal relationships between an organism and its
environment, but research on the thermal energy exchange of both plants and
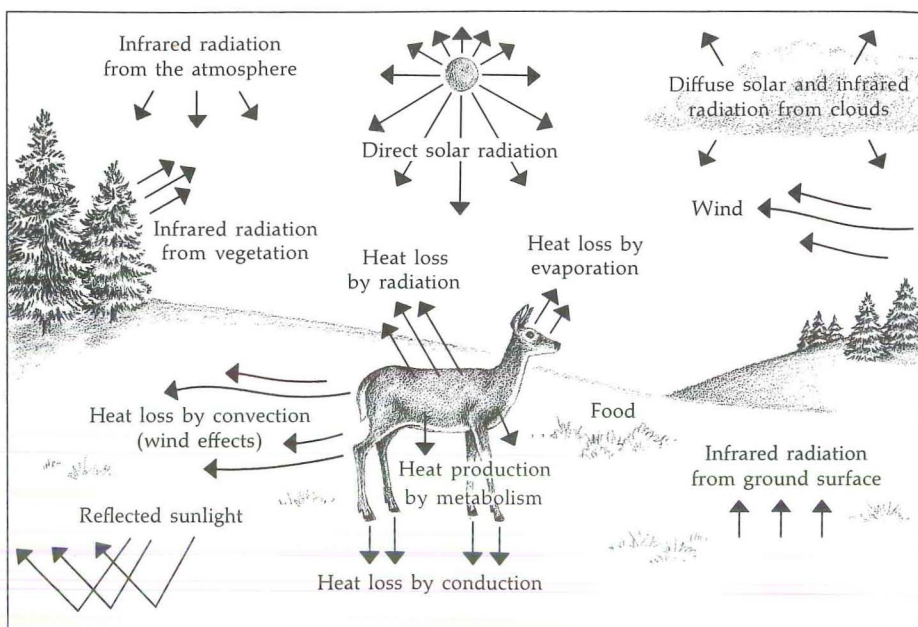animals has provided insight into the mechanisms involved.

FIGURE 6-1.   The thermal energy exchange between an animal and its environment includes radiation, conduction, convection, and evaporation as the four basic modes of heat transfer.

6-2   RADIANT ENERGY EXCHANGE

Radiant energy exchange occurs between two surfaces as each surface emits energy at wavelengths that are dependent on the temperature of the emitting surface. Radiant energy travels through those media that are transparent, neither reflecting nor absorbing the radiation. A complete vacuum presents no obstructions to radiant energy exchange. A discussion of the basic characteristics of radiant heat exchange follows.

THE ELECTROMAGNETIC SPECTRUM.   The electromagnetic spectrum includes wavelengths as long as hundreds of miles and as short as 1×10^{-10} cm (0.0000000001 cm). Between these two extremes there are, in order of decreasing wavelength, the radio waves that are received by standard radio sets, the short waves, the infrared portion (perceived as heat), visible light, ultraviolet rays, x rays, and gamma rays. The radiant energy that is important in the maintenance of homeothermy includes the wavelengths in the visible portion and the longer wavelengths in the infrared portion of the electromagnetic spectrum.

Both the amount of radiation from an object and the wavelengths emitted are functions of the temperature of the object. The Stefan-Boltzmann law states that the amount of radiation emitted from a black body is directly proportional to the fourth power of the absolute temperature (°K) of the object. A black body is an object that absorbs all the radiant energy that reaches its surface. If a surface

is not a black body, the amount of energy that can be absorbed is expressed as a coefficient ranging from zero to one. The absorption coefficient for long-wave radiation is also equal to the emissivity of that surface, since it is equally as good an emitter of long-wave radiation as it is an absorber. This relationship can be expressed with equation (6-1).

$$Q_r = \epsilon \sigma T_s^4 \tag{6-1}$$

where:

Q_r = radiant energy emitted in kcal m^{-2} hr^{-1}
ϵ = emissivity (range from zero to one)
σ = Stefan-Boltzmann constant = 4.93×10^{-8} kcal m^{-2} hr^{-1}
T_s = surface temperature of the object in °K

The Wien displacement law states that the wavelength (λ) of maximum intensity that is emitted from the surface of a black body is inversely proportional to the absolute temperature of the body [equation (6-2)].

$$\lambda \text{ max } (\mu) = 2897 \ T^{-1} \tag{6-2}$$

Thus a very hot surface emits shorter wavelengths, while a cooler surface emits longer wavelengths.

SOLAR RADIATION. The wavelength of maximum emission from the sun is 0.5μ, which is in the visible portion of the spectrum (Sellers 1965). Sellers points out that 99% of the sun's radiation is in the wavelength range of 0.15μ to 4.0μ, including 9% in the ultraviolet (<0.4μ), 45% in the visible (0.4μ to 0.74μ), and 46% in the infrared (>0.74μ).

The amount of energy reaching a surface perpendicular to the rays of the sun at the outer limits of the earth's atmosphere is called the solar constant. Textbooks published prior to the mid-fifties included a value for the solar constant of 1.94 calories per square centimeter per minute. This value has been revised by Johnson (1954) to 2.00 calories per square centimeter per minute. It actually varies by about 1.5% because of differences in the total energy emanating from the sun and because of variation in the distance between the earth and the sun.

Not all of the sun's energy reaches the surface of the earth. Some of it is reflected into space or absorbed by dust particles and moisture in the atmosphere. On a clear day, a high percentage of the solar radiation is transmitted through the atmosphere. With a completely overcast sky, no direct solar radiation penetrates the cloud cover.

There are three possible pathways for radiant energy to take once it reaches a plant or animal. It may be reflected from the surface, it may be absorbed by the surface, or it may be transmitted through the material (Figure 6-2). Energy that is reflected from the surface is of no thermal benefit to an animal or plant. Reflected energy in the visible portion of the spectrum is detected as shades of gray or as color, depending on the receptors of the organism detecting the light energy. Transmitted solar energy is of no value to an animal, and all animals
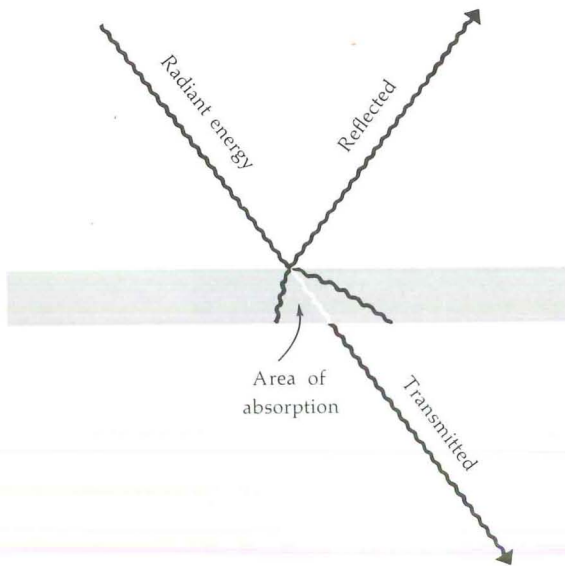
FIGURE 6-2. The three pathways for radiant energy reaching a plant or an animal.

except the smallest protozoans are essentially opaque. The leaves of plants, however, transmit some solar energy. Absorbed energy becomes a part of the thermal and physiological regime of an organism, and the quantity and distribution of absorbed radiant energy is of interest to the physiologist and the ecologist.

The amount of energy absorbed by the hair surface of a mammal depends on the spectral characteristics of the hair and the angle at which the solar energy strikes the surface. The absorption coefficients for cattle have been measured by Riemerschmid and Elder (1945) and are shown in Figure 6-3. White coats absorb less and reflect more solar energy; black coats absorb the most solar energy. The greatest amount of energy is absorbed when the solar radiation strikes perpendicular to the surface; no absorption takes place when the rays are parallel to the surface. Inclination of the hair, the smoothness or curliness of the coat, and seasonal changes in the characteristics of the coat have little effect on the absorptivity. Since animals are not plane surfaces but have a complicated geometry, the absorption characteristics of a whole animal include all angles from 0 to 90 degrees. The distribution of solar radiation on the surface of an animal is called the solar radiation profile and is discussed later in the chapter.

INFRARED RADIATION. Radiation of wavelengths longer than those in the visible portion of the spectrum is called infrared radiation. The same pathways of reflection, absorption, or transmission are followed as for solar radiation. All objects emit infrared radiation according to the Stefan-Boltzmann law [equation (6-1)]. The energy of the shorter wavelengths characteristic of the visible portion of the spectrum that is absorbed by an object is reradiated as infrared energy according to the Stefan-Boltzmann law.

ATMOSPHERIC TRANSMISSION AND ABSORPTION CHARACTERISTICS. The clear atmosphere is nearly transparent to the wavelengths within the visible portion of the
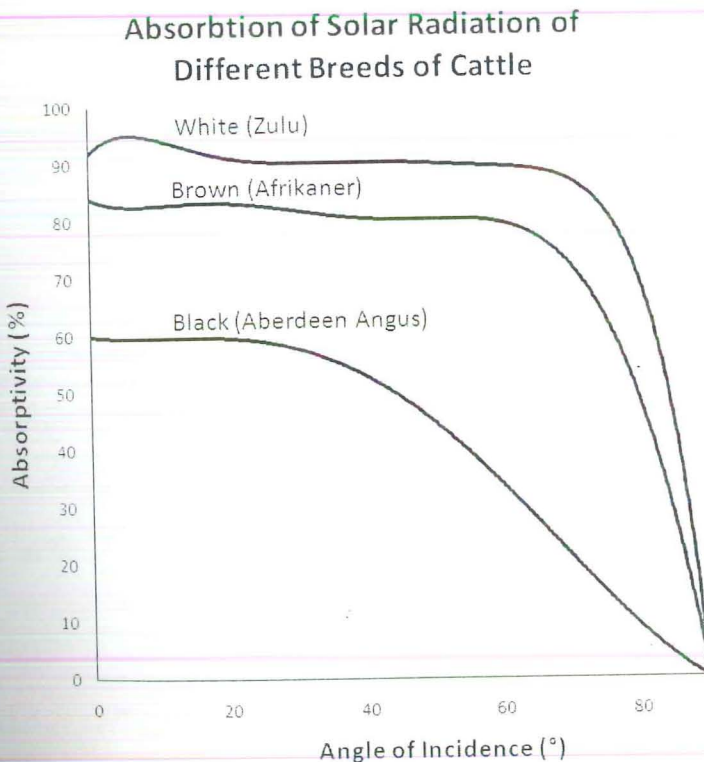
electromagnetic spectrum. Emissivity and absorption characteristics of the atmosphere in the infrared portion of the electromagnetic spectrum are dependent on the composition of the atmosphere. Water vapor and carbon dioxide have high emissivities and absorptivities at certain wavelengths, so the transmission of infrared energy through the atmosphere at those wavelengths is very low. Cloud cover has essentially 100% absorptivity. Some wavelengths are not absorbed by the atmosphere and hence pass through the "atmospheric windows" (Figure 6-4).

Solar radiation that is transmitted through the atmosphere during daylight is partially absorbed by the earth's surface, and the heat energy is reradiated at longer wavelengths. Some of these wavelengths are transmitted through the atmospheric windows and their heat energy is dissipated into space.

If the atmosphere were completely transparent to radiation, the earth would be considerably warmer during the day and colder during the night. The blanketing effect of the atmosphere results in the maintenance of relatively stable climates. The surface of the moon has fluctuations in temperature from about 240°F to −260°F because there is no atmosphere to buffer the radiant heat exchange.

FIGURE 6-3. The absorption of solar radiation by three breeds of cattle at different angles of incidence. (Adapted from "The absorbtivity for solar radiation of different coloured hairy coats of cattle" by G. Riemerschmid and J.S.Elder. *Onderstepoort J. Vet. Sci. Animal Ind.* 1945.)

Absorbtion of Solar Radiation of Different Breeds of Cattle

White (Zulu)

Brown (Afrikaner)

Black (Aberdeen Angus)
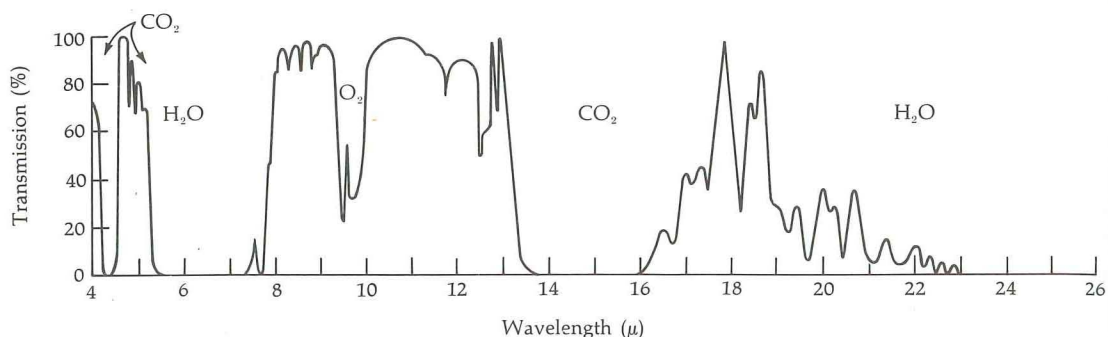
Absorptivity (%)

Angle of Incidence (°)

FIGURE 6-4. Atmospheric transmission in the infrared portion of the electromagnetic spectrum. (From Gates 1962.)

The blanketing effect of the earth's atmosphere is often called the "greenhouse effect." A greenhouse transmits solar radiation through glass, and this radiant energy is absorbed by the objects inside. This energy is reradiated at longer wavelengths, but since glass is not highly transparent to infrared waves, some of the energy is reflected back from the glass and retained inside the greenhouse. This effect is also obvious in an automobile when the windows are closed on a hot, sunny day.

ATMOSPHERIC EMISSION. The amount of infrared radiation emitted from the atmosphere during different weather conditions has been measured by meteorologists, and radiation charts for estimating atmospheric radiation from certain meteorological parameters have been constructed. Empirical equations have also been used to estimate the radiation exchange. They have been criticized because they are based on the assumption that outgoing radiation at any given point is determined chiefly by thermal conditions at the surface (Sellers 1965). If empirical equations are applied to specific atmospheric conditions, such as a clear sky, the results are quite reasonable owing to the "screen effect" discussed by Swinbank (1963). The screen effect results from radiation exchange within the atmosphere that limits the effective radiating height of an air column to a few feet. Swinbank presents data that show this to be the case at higher altitudes also, indicating that the total height of the atmospheric column is not particularly important. Empirical equations for given habitats and atmospheric conditions are presented later in this chapter (see Figure 6-5 and Table 6-1).

Infrared energy flux between the atmosphere, overhead vegetative cover, and the earth's surface can be divided into downward and upward components. The difference between the two is called the *net* radiation, and the sum of the two is the *total* radiation. Before considering the ecological implications of these two, let us look at some downward and upward flux measurements under different sky conditions and in different habitats.
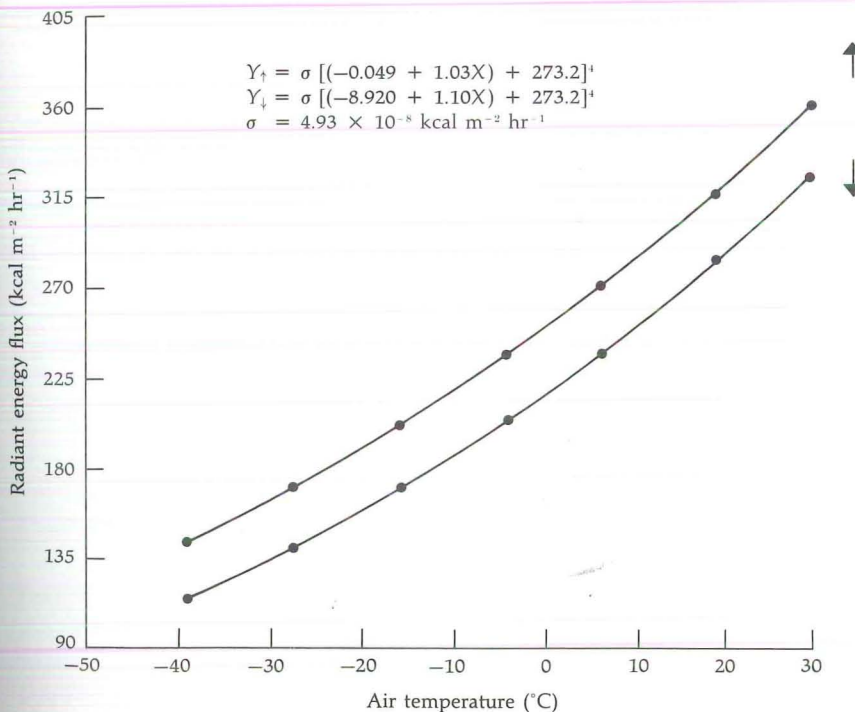
Extensive field measurements by the author in both Minnesota and New York indicate that the amount of radiant energy flux under clear skies at night can be predicted with considerable precision if the atmospheric temperature is known. This method was used by Swinbank (1963) also.

Radiant energy flux under clear skies at night in open fields in western Minnesota near Kensington, eastern Minnesota near Bethel, and western New York in Lansing in both winter and spring is shown in Figure 6-5. Some significant conclusions can be drawn from this figure. The downward radiation during clear nights is obviously less than the upward radiation; the clear night sky is cold. The upward radiation—a function of surface (snow or vegetation) temperature and emissivity—is very closely related to air temperature. This is shown in the regression equation for upward flux where the slope of the line is 1.03, or essentially 1.0, and the intercept is −0.049, or just about zero. Thus, radiation from a snow surface can be approximated by the use of air temperature for T (in °K) in equation (6-1). This assumes that the snow-surface temperature is equal to air temperature, which is a good approximation up to 0°C. The data for upward radiation in Figure 6-5 and Table 6-1 clearly indicate this relationship. Less reflective and more absorbent surfaces, such as soil, will show greater temperature differences, especially during the day and in the early part of the evening before radiational cooling has occurred.

The relationship between the radiant temperature of the sky and air temperature is shown in Figure 6-6. The regression equations and correlation coefficients for the four different periods of measurement are listed in Table 6-1. Note the

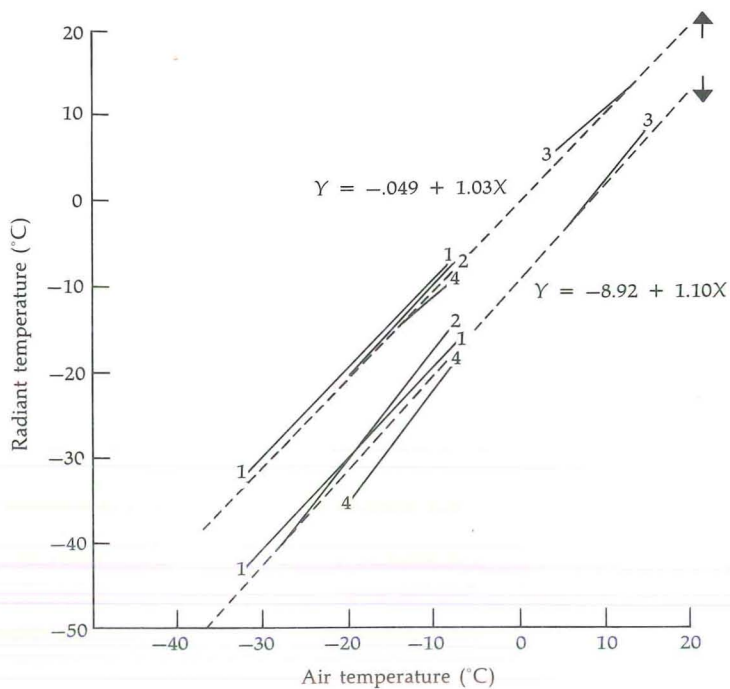FIGURE 6-5. Downward and upward radiation flux in open fields under clear night skies. (From Moen and Evans 1971.)

$$Y_\uparrow = \sigma \left[(-0.049 + 1.03X) + 273.2\right]^4$$
$$Y_\downarrow = \sigma \left[(-8.920 + 1.10X) + 273.2\right]^4$$
$$\sigma = 4.93 \times 10^{-8} \text{ kcal m}^{-2} \text{ hr}^{-1}$$

FIGURE 6-6. The relationship between radiant temperature and air temperature under clear skies at night.

TABLE 6-1 REGRESSION EQUATIONS AND CORRELATION COEFFICIENTS FOR THE TEMPERATURE MEASUREMENTS IN FIGURE 6-6

Location	Upward or Downward	Radiant Temperature Formula	Correlation Coefficient
Kensington, Minn. (winter)	Upward	$Y = -0.025 + 1.015X$	0.994
	Downward	$Y = -9.202 + 1.039X$	0.968
Bethel, Minn. (winter)	Upward	$Y = 0.490 + 1.059X$	0.993
	Downward	$Y = -4.611 + 1.264X$	0.935
Lansing, N.Y. (spring)	Upward	$Y = 1.065 + 0.947X$	0.995
	Downward	$Y = -10.736 + 1.288X$	0.994
Lansing, N.Y. (winter)	Upward	$Y = -1.568 + 0.948X$	0.984
	Downward	$Y = -8.888 + 1.285X$	0.973
All measurements	Upward	$Y = -0.0491 + 1.030X$	0.999
	Downward	$Y = -8.9150 + 1.103X$	0.995

SOURCE: Moen and Evans 1971.

greater variation in the radiant temperature of the sky than in the radiant temperature of the snow or plant surfaces. All measurements were made under clear skies, but differences in the atmospheric temperature profile and in the vapor pressure of the atmosphere contribute to variation in the downward radiation flux. Additional field measurements by the author show that, under cloudy skies, the radiant temperature of the atmosphere is very nearly equal to air temperature.

What is the ecological significance of net and total radiation flux? First of all, the application of these terms to the *atmospheric energy balance* is of interest when the energy balance of the earth is being considered. In that context, they are meteorological terms and not ecological terms. To illustrate, the downward radiation flux under a clear sky with an air temperature of $-30°C$ is 141 kcal m^{-2} hr^{-1} (see Figure 6-5), the upward flux is 169 kcal m^{-2} hr^{-1}, the total is 310 kcal m^{-2} hr^{-1}, and the net is -28 kcal m^{-2} hr^{-1}. At an air temperature of $+20°C$, the downward flux is 366 kcal m^{-2} hr^{-1}, the upward is 325 kcal m^{-2} hr^{-1}, the total is 691 kcal m^{-2} hr^{-1}, and the net is -41 kcal m^{-2} hr^{-1}. Note that there is a larger negative balance at the higher temperatures, but the total flux is more than two times greater at $+20°$ than at $-30°C$. The total radiant energy flux strikes the surface of plants and animals, and the additional radiation at warmer temperatures results in a greater amount of absorbed radiation by the organisms. Geometric considerations necessary to calculate the absorbed thermal radiation are very complex. The ecologist is interested in the exchange of heat between organisms and environment, just as the meteorologist is interested in the exchange of heat between the earth, the atmosphere, and the exosphere. Thus a careful distinction must be made between the net energy balance of the earth and the net energy balance of an organism living on the earth.

The amount of infrared energy from three different cover types under clear nocturnal skies in the winter is distinctly different. Of the three types indicated in Figure 6-7, the least amount of downward radiation comes from the clear sky and the most from the cedar (*Thuja occidentalis*) cover. The differences between them are related to the density of the overhead cover. The density, however, is not the density viewed from the ground vertically through the canopy at a number of points; rather it is the effective thermal density as measured from a single location in the stand. At angles of less than $90°$, the effective density of the stand increases in a manner similar to a "venetian blind effect." For example, the cedar canopy in the Cedar Creek Natural History Area in Minnesota occluded from 50% to 80% of the sky within a $35°$ field of view above the radiometer. In the upland hardwood stand, only 10% to 50% of the sky was occluded in a $35°$ field of view above the radiometer, but the downward radiation was midway between the downward flux in cedar cover and from the clear sky in an open field. This illustrates that, at increasing angles from the zenith, a canopy becomes optically and thermally more opaque. Since the radiometer senses almost the entire hemisphere, the measured downward flux is considerably higher than the canopy density viewed vertically would indicate. The effect of this radiant energy on the snow is apparent in the formation of icy crusts in open fields and the looser, less crusty snow found in forest stands.
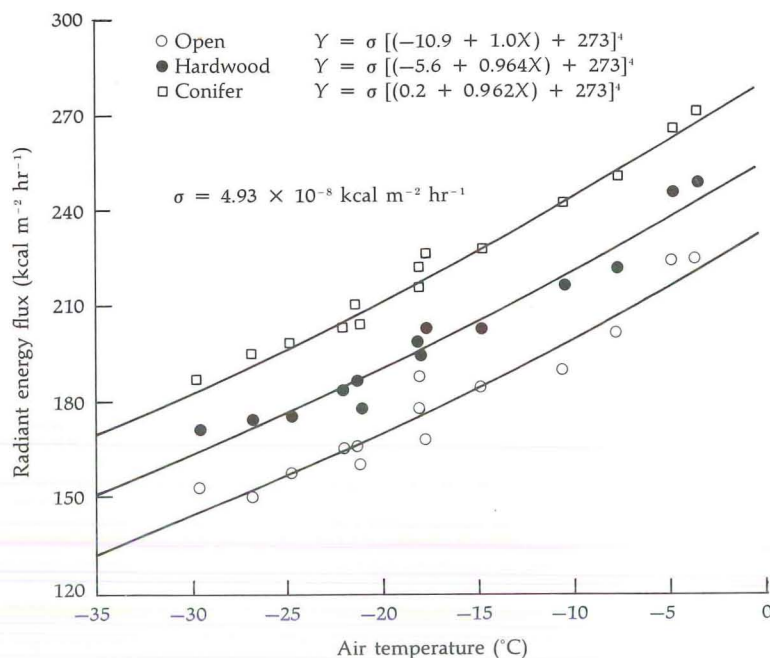
FIGURE 6-7.   Downward radiation flux under clear skies at night in three cover types on the Cedar Creek Natural History Area, Minnesota. (From Moen 1968, *J. Wildlife Management.*)

What limits are imposed on the amount of radiation from vegetation and snow in the canopy? Complete obstruction of the sky results in a maximum amount of downward radiation, equal to the flux from a completely overcast sky when the vertical temperature profile from the ground surface into the cloud cover is isothermal. An animal in this circumstance is exposed to a homogeneous radiant environment in all directions, very similar to a chamber with uniform temperature distribution. The actual thermal benefits derived from this radiant energy cannot be determined until the interaction between radiation and convection in the insulating layer of hair has been analyzed.

RADIATION FROM PHYSICAL AND BIOLOGICAL OBJECTS.   The amount of thermal radiation from physical and biological objects is a function of their emissivity (ϵ) and temperature (°K). The emissivity is an important part of the equation when it is applied to biological organisms that have a limited surface area. Potential error in radiation measurements that may be introduced by making false assumptions about emissivity of plants is discussed in Fuchs and Tanner (1966). Porter (1969) discusses the importance of considering emissivity in making measurements in a chamber. The general rule to follow is that there are larger differences between apparent radiant temperature and real radiant temperature as the difference between the radiant temperatures of the target organism and the

environment becomes greater. The importance of radiant energy exchange in the entire thermal balance also increases under these conditions of greater temperature differences.

EMISSIVITY AND REFLECTIVITY OF SNOW.   The snow surface is composed of small ice crystals, making it extremely rough. The rough snow surface is almost a perfect black body for the absorption and emission of long-wave radiation. Since the temperature of snow is limited to a maximum of 0°C, the maximum intensity of radiation that may be emitted is 27.45 ly hr^{-1} (calories cm^{-2} hr^{-1}) or 274.48 kcal m^{-2} hr^{-1}, calculated from equation (6-1).

Snow is a good reflector of radiant energy in the visible portion of the electro-magnetic spectrum. Freshly fallen snow may have an albedo of 75%–95%, although snow several days old may reflect 40%–70% of the short-wave radiation (Sellers 1965).

The infrared emissivities of most biological materials are close to 1.0. Several hair surfaces have been tested, with measured emissivities ranging from 0.92 to 1.0 for several species (Table 6-2). An emissivity of 1.0 is a satisfactory first approximation at this point. The error will be quite small in the range of temperatures experienced by animals in natural habitats.

RADIANT TEMPERATURE IN RELATION TO AIR TEMPERATURE.   There is a predictable relationship between the radiant temperature (T_r) of an animal and the air temperature (T_a) if environmental radiation striking the animal's surface and wind flow over the surface are known. This is illustrated in Figure 6-8 for deer and sharp-tailed grouse. Note that the radiant temperature of the animal's surface drops as the air temperature drops but in both cases the difference between T_r and T_a is greater at colder temperatures. This is an important consideration in later thermal analyses. For now, remember that as the air temperature drops, the radiant surface temperature of an animal also drops, but at a slower rate. This results in a relatively warmer radiant surface when exposed to a colder air temperature.

Variations in wind velocity and environmental radiation affect the relationship between T_r and T_a. The effects of different wind velocities across the surfaces of deer and grouse simulators are shown in Figure 6-9 and 6-10, respectively. At −20°C, the radiant temperature of deer is about −6°C when the velocity of the wind is less than 1 mi hr^{-1}, but −14°C when the velocity is 14 mi hr^{-1}. This drop of eight degrees in the surface temperature is due to the increased convection losses at the higher velocities. The nonlinear effect of wind is also observed when a change from 0 to 8 mi hr^{-1} at −20°C reduces the radiant temperature by 5.9 degrees, but a change from 8 to 14 mi hr^{-1} reduces it further by only 2.4 degrees (Figure 6-9).

The dashed line in Figure 6-9 illustrates radiant temperature in relation to air temperature for a wind velocity of 0 mi hr^{-1} when the sky acts as a cold heat sink. The radiant temperature is depressed when there is no wind blowing across

TABLE 6-2 INFRARED EMISSIVITIES OF DIFFERENT HAIR OR FEATHER SURFACES

Species	Condition of Pelage	Emissivity
Willow Ptarmigan†		
(*Lagopus lagopus*)	On frozen carcass	.98
Snowshoe hare†		
(*Lepus americanus*)	On frozen carcass	.99
Cottontail rabbit*	Dorsal sample	0.97–0.98
(*Sylvilagus floridanus*)	Ventral sample	0.92–0.93
Barren ground caribou†		
(*Rangifer arcticus*)	Frozen, off carcass	1.00
Sea otter†		
(*Enhydra lutris*)	Tanned	0.98
Grey wolf†		
(*Canis lupus*)	Tanned	0.99
Beaver†		
(*Castor canadensis*)	Tanned	0.99
Beaver†		
(*Castor canadensis*)	Dry	1.00
Lynx†		
(*Lynx canadensis*)	Tanned	1.00
Red fox†		
(*Vulpes fulva*)	Tanned	0.98–1.00
Marten†		
(*Martes americana*)	Tanned	1.00
Bobcat†		
(*Lynx rufus*)	Tanned	1.00
Flying squirrel*	Dorsal sample	0.95
(*Glaucomys volans*)	Ventral sample	0.95–0.99
Woodchuck*		
(*Marmota monax*)	Dorsal sample	0.98
Red squirrel*	Dorsal sample	0.95–0.98
(*Tamiasciurus hudsonicus*)	Ventral sample	0.97–1.00
Grey squirrel*	Dorsal sample	0.99
(*Sciurus carolinensis*)	Ventral sample	0.99
Mole*		
(*Scalopus aquaticus*)	Dorsal sample	0.97
Deer Mouse*		
(*Peromyscus sp.*)	Ventral sample	0.94

† Data from Hammel 1956.
* Data from Birkebak, Birkebak, and Warner 1963.

the hairy surface. At wind velocities of 1 mi hr^{-1} or more, the effect of the cold sky disappears since the air temperature is the dominant thermal factor. This can be attributed to advection, which is basically the process of convection discussed in Section 6-4.

$Y = 6.559 + 0.944X$
$n = 74$

A

Air temperature (°C)

Head $Y = 19.05 + 0.54X$
       $n = 66$
       $r = 0.977$

Body $Y = 5.25 + 0.87X$
       $n = 222$
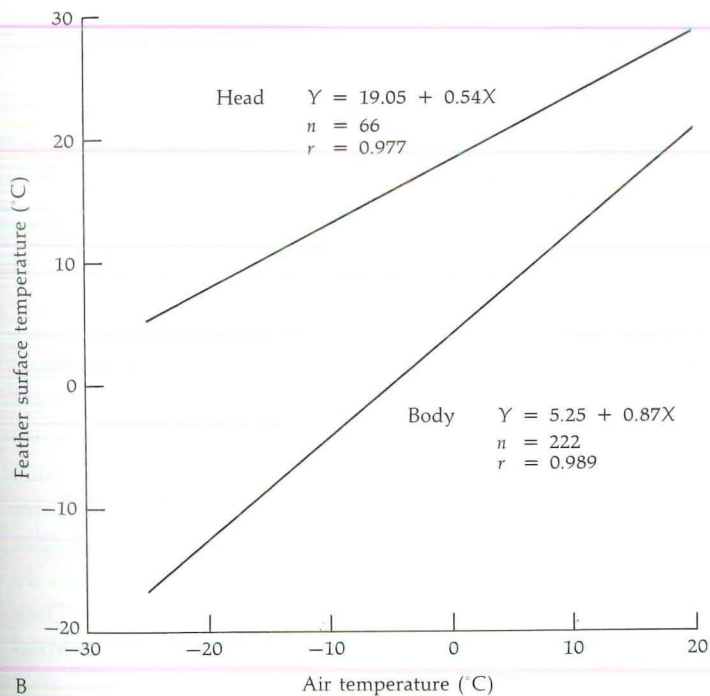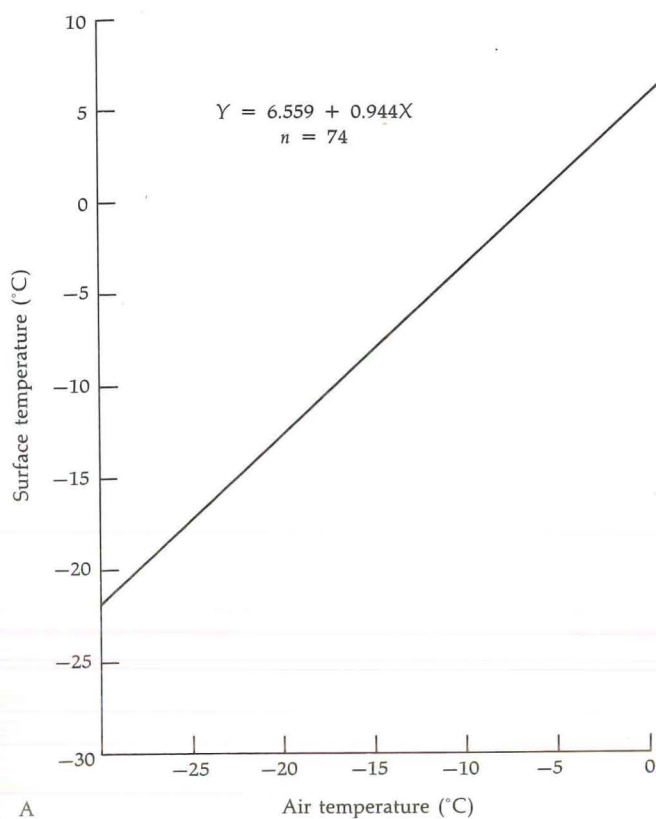 $r = 0.989$

B

Air temperature (°C)

FIGURE 6-8. Radiant surface temperature related to air temperature for (A) deer and (B) grouse. (Data on deer are from Moen 1968 and on grouse from Evans 1971.)
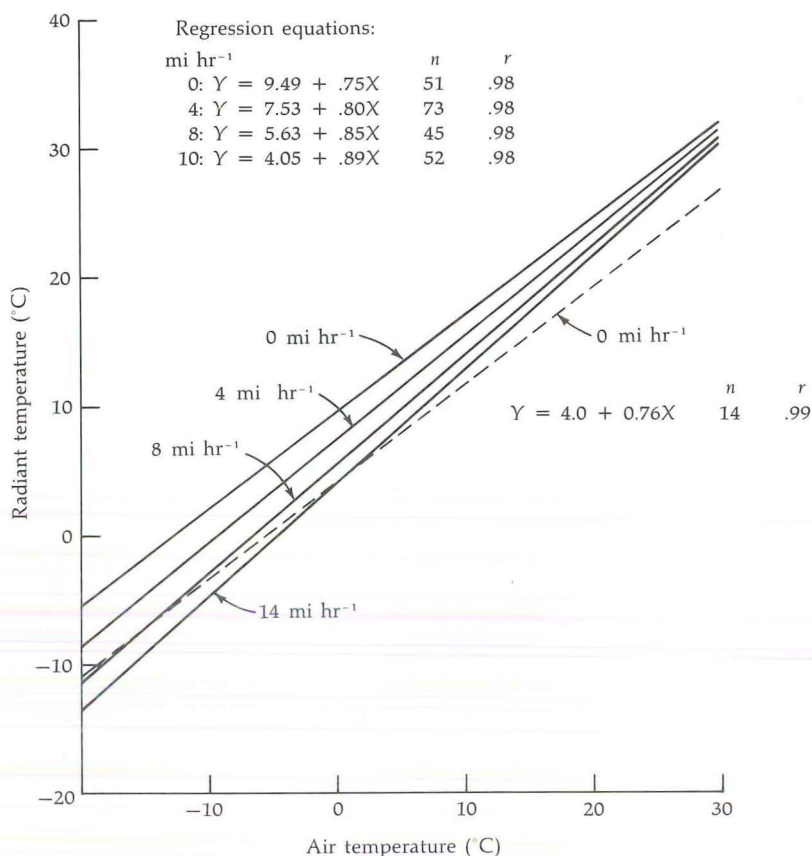
FIGURE 6-9. Radiant temperature related to air temperature for the white-tailed deer simulator in the TMST with two levels of environmental radiation. Solid line: T_r when $T_e = T_a$ in test chamber. Dashed line: T_r when $T_e = T_a - 10$ in test chamber. (Additional data are given in Appendix 4.)

The radiant temperature of an animal's surface rises when the animal is exposed to higher levels of environmental radiation. The surface temperature of an adult male pheasant, for example, was 45°C when its back was exposed at right angles to a bright afternoon sun. No wind was blowing past the surface at the time. Since the body temperature of a pheasant is about 40°C, the radiant surface was warmer than the body itself. When a cloud shaded the sun and a slight wind blew over the pheasant's surface, the radiant temperature dropped to 20°C, which was about equal to the air temperature, in a manner of seconds. This indicates the variability of the animal's radiant temperature, which changes with changes in wind, radiation, temperature, and other thermal factors. Hair and feathers do not merely provide insulation from the cold, but from the heat as well. They tend to ameliorate the thermal regime of the body proper by buffering the thermal variations.

The effect of direct solar radiation on the radiant temperature over the entire surface of a plant or animal is not uniform because both the color of this surface
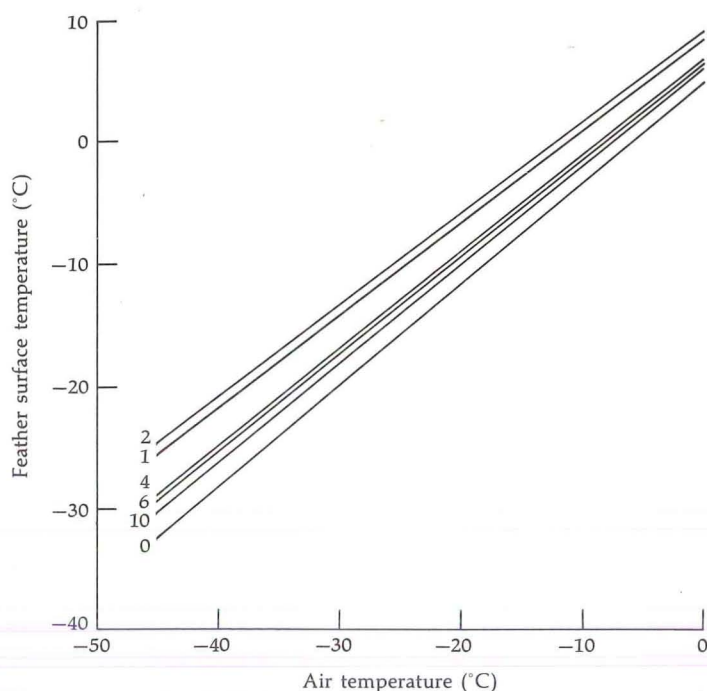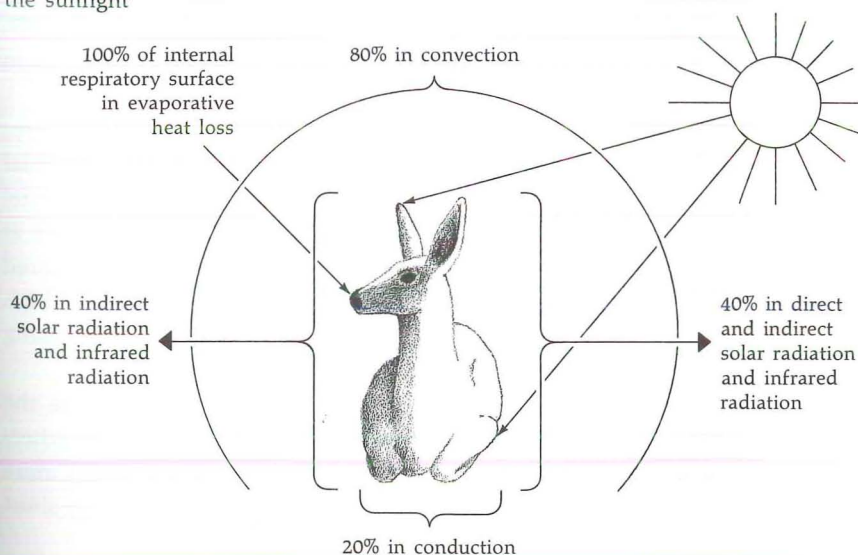
FIGURE 6-10. Effect of air temperature and wind velocity on feather surface temperatures. Prediction formulas are listed in Appendix 4. (Evans 1971.)

and the angle of the rays striking the surface are important in determining just how much solar energy is absorbed. For example, a deer bedded in the sun (Figure 6-11) might have 40% of its surface exposed to direct solar radiation, 80% exposed to indirect solar radiation, and 80% exposed to infrared radiation. These differ-

FIGURE 6-11. The relative proportions of the surface area of a deer bedded in the sunlight

100% of internal respiratory surface in evaporative heat loss

80% in convection

40% in indirect solar radiation and infrared radiation

40% in direct and indirect solar radiation and infrared radiation

20% in conduction

ences result in different radiant temperatures, but they act in combination with the distribution of tissue metabolism beneath the hair surface as well as with the distribution of blood. The radiant temperature distribution of an animal exposed to only infrared radiation at night is much simpler since the hair surface is almost a black body and infrared energy is much more uniformly distributed in the environment than is solar energy. The biological characteristics of tissue metabolism and blood flow still contribute to variations, however.

Radiant temperatures of leaf surfaces can be measured remotely with an infrared thermometer just as animal surfaces are measured. Radiant temperature and air temperature are much more similar for plants than for animals because only a small amount of metabolic heat is released inside the leaf. In homeothermic animals, however, there is heat flow from the many exothermic reactions inside the animal to the outside through a layer of insulating hair or feathers. Thus the surface temperature of an animal is dependent on blood flow beneath the skin, local tissue metabolism, and on the quality of the insulating pelage. In a plant, the surface temperature is dependent primarily on the interactions between thermal parameters alone, with virtually no input from metabolic reactions within the leaf.

The considerations described above are indicative of the complexity facing the ecologist who looks at the way things function in the real world. There is so much interaction that it is difficult and frustrating to talk about isolated things because they never function in isolation! Yet, in writing a general text for students of ecology, it is necessary to cover things one at a time, synthesizing more and more as knowledge and understanding accumulate.

6-3 INSTRUMENTATION FOR MEASURING RADIATION

The basic design of equipment for measuring radiation in the visible and infrared portion of the spectrum is quite simple. An economical radiometer (Figure 6-12), designed by Suomi and Kuhn (1958) and described in greater detail by Tanner, Businger, and Kuhn (1960), has the necessary components for measuring radiation (Figure 6-13).

The sensing element is the basic component of an instrument that measures radiation. This sensor may have spectral characteristics that measure only solar or long-wave thermal radiation. A black paint such as Minnesota Mining Nextel Velvet Coating (101-C10 Black) has a quoted emmissivity of 0.9 or better at wavelengths from 2 to 35 microns. Thus it is almost a black body in the infrared portion of the spectrum. White or silver paints have low absorptivities and high reflectivities in the visible portion of the spectrum. These are used on the sensing elements of instruments that separate solar from long-wave radiation.

A thermometer, thermocouple, or thermistor may be used to measure the temperature of the sensing element. Commercial instruments usually have thermocouples or thermistors as temperature sensors. They respond to changes more quickly than thermometers do, an advantage if the radiation flux varies over short

FIGURE 6-12.   An economical radi-
ometer in a maple-basswood
stand.

FIGURE 6-13.   The components of an economical homemade radiometer. The
dimensions suggested can be altered if necessary.
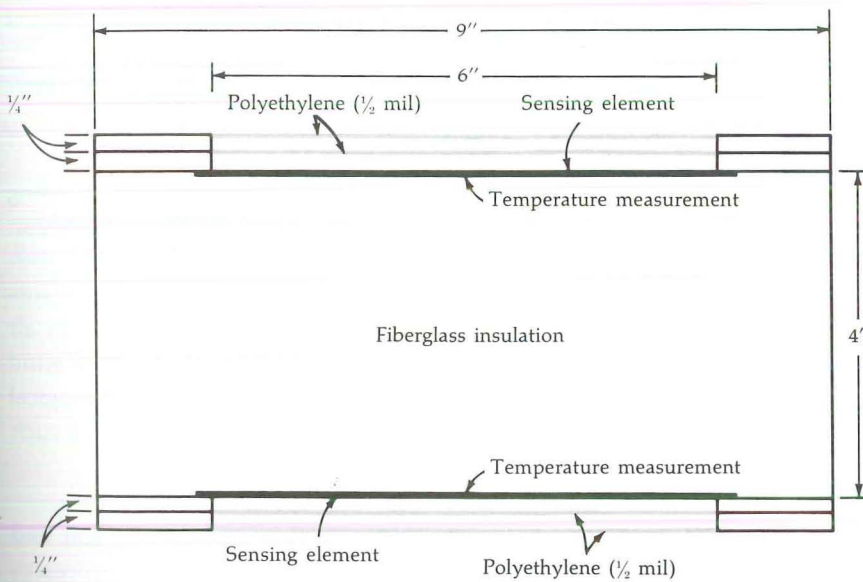
time spans. Thermometers do not require a power source, making them more convenient for field use.

Another component is the shield over the sensing element. The shield may act as a filter that permits only certain wavelengths to reach the sensing element. Polyethylene, for example, is used in the economical radiometer for measuring long-wave radiation because it has a high transmission coefficient in the infrared. Glass would not be suitable because it is not transparent in the infrared. The shield on the economical radiometer is flat. On some instruments it is hemispherical, which is better for measuring solar radiation because the reflectivity of a flat surface increases as the angle of incidence decreases.

Another function of the shield is to protect the sensing element from wind. A sensing element warmed by the sun is cooled if wind blows over its surface. This results in an underestimation of the radiant energy. Actually, free convection occurs at the surface of even an enclosed sensor, but this is fairly negligible with proper instrument design. Some instruments are "ventilated," with a fan providing a constant wind effect that is corrected for in the electronic circuitry. The insulation in the economical radiometer reduces heat flow between the top and bottom of the sensing elements. Any commercial insulation with a known thermal conductivity can be used. A correction for one-dimensional heat flow through the insulation from one sensor to the other is made.

The equations for calculating radiation flux with the economical radiometer are shown in Appendix 2. Good sources for the design of other radiometers are Gates (1962) and Platt and Griffiths (1964).

The accuracy of different instruments is an important consideration before selecting one for field or laboratory use. The accuracy required is related to the use of the data, so selection should not be made on the basis of stated accuracies alone. The economical radiometer is sufficiently accurate for measuring radiation flux in different habitats at night, especially if several instruments are used and the results are averaged, since the application of radiation data to animals is not a particularly precise procedure.

6-4 CONVECTION

Heat energy may be removed from the surface of an object by fluid (air) flowing over the surface. This process is called convection. Two types of convection occur: free convection (also called natural convection) and forced convection. Free convection occurs when temperature differences in the boundary layer of air surrounding an object cause a movement of the air in response to changes in air density. Forced convection occurs when external pressure differences cause wind to blow past the object. Before considering convection in relation to biological organisms, let us consider air flow over different surfaces and past objects such as windbreaks and animals.

AIR MOVEMENT.   The air surrounding an organism has certain physical and thermal characteristics that should be understood before the convection processes are described. One of these is the presence of a velocity boundary layer (Figure

6-14), which develops because of surface friction. At the surface, the velocity of air flow is, theoretically, zero. The velocity increases at greater distances from the surface, and the point at which maximum velocity is reached marks the beginning of the free air stream. The depth of the boundary layer depends primarily on the roughness of the surface.

MEAN VELOCITY WIND PROFILES.   The mean horizontal velocities can be calculated with equation (6-3) (from Sellers, 1965, with modification).

$$U_z = (u_*/k) \ln (Z/Z_0) \qquad (6\text{-}3)$$

where:

U_z = wind velocity at height Z
u_* = friction velocity
k = von Karman constant = 0.4
Z = height in cm
Z_0 = roughness parameter of surface; the height at which velocity is zero

The reduction in wind velocity owing to friction will be greater over a rough, vegetation-covered surface than over a smooth, snow surface. If the wind velocities were the same, say, 622 cm sec^{-1} (13.9 mi hr^{-1}), at a height of 2 meters over both types of surfaces, the velocity at a height of 75 cm (or around the top of the back of an average deer) would be about 433 cm sec^{-1} (9.7 mi hr^{-1}) over

FIGURE 6-14. Predicted vertical profiles of mean wind velocity over grass that is 60–70 cm in height and over a snow surface. The profiles within the vegetation are based on data on corn. (From Stevens and Moen 1970.)
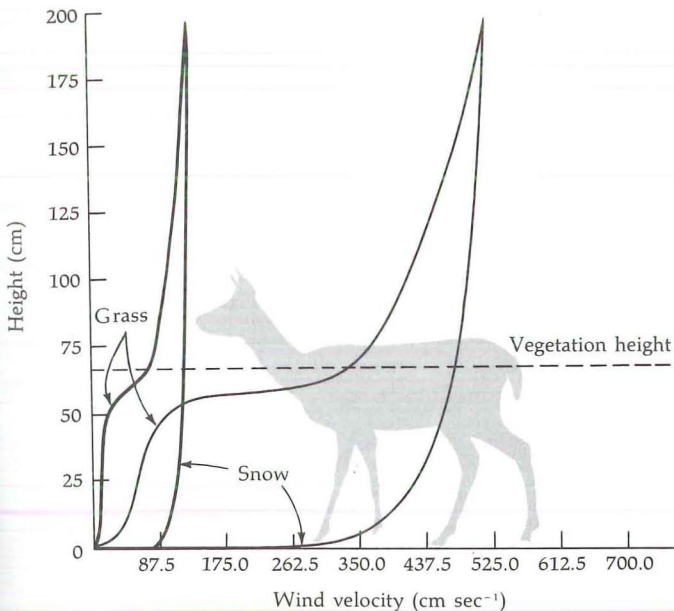
grass that is 60–70 cm high, and 572 cm sec^{-1} (12.8 mi hr^{-1}) over a snow field (see Figure 6-14). The shape of the velocity profile within the vegetation depends on the life-form and density of the vegetation. The profile within the vegetation in Figure 6-14 is approximated for grass from data for air flow through a corn field (Ordway 1969). Similar profiles are shown by Plate and Quraishi (1965) for corn and wheat.

Mean velocity profiles give the impression that wind flow is layered or *laminar*. Actually, wind flow in the field is three-dimensional. There is air movement on a horizontal plane in one direction (U_u), perpendicular to U_u but in the same plane (U_w), and vertical (U_v), or perpendicular to the plane of U_u and U_w.

Three-dimensional wind flow is caused by friction between air molecules and the ground surface, causing turbulence, or a mixing of the air. Turbulent flow can be described in terms of scale and intensity. Turbulence scale is a measure of the size of the turbulent wind mass, and turbulence intensity is the magnitude of fluctuations relative to the average or mean wind speed. In the field, vegetation and objects on the ground impede the wind flow, reducing mean wind velocity and increasing the turbulence. The amount of turbulence created depends on the physical characteristics of the vegetation and of the ground surface.

Animals in natural habitats are not exposed to a single wind velocity but to a range of velocities in all three dimensions that are a function of the physical characteristics of the environment. This was illustrated in Figure 5-10, in which tiny aerodynamically stable bubbles follow the flow of air through a model windbreak. Note the downward wind flow over the back of the deer, the reversal in wind direction behind the deer, and the development of the profile on the right edge of the photograph.

An individual animal also presents an obstruction to wind, creating small wind patterns that are dependent on its body shape and posture. Analyses of the patterns of wind flow around a model white-tailed deer in a bedded posture indicate that the air flows smoothly around the windward side of the animal, with a turbulent zone on the lee side of the animal (Figure 6-15A). A quail causes a spiraling effect when facing directly into the wind (Figure 6-15B).

6-5 CONVECTIVE HEAT LOSS

The amount of heat that is removed from an object by convection is a function of the factors expressed in equation (6-4).

$$Q_c = h_c At(T_s - T_a) \tag{6-4}$$

where

Q_c = calories of heat transferred by convection
h_c = convection coefficient
A = area
t = time
T_s = temperature of the surface of the convector
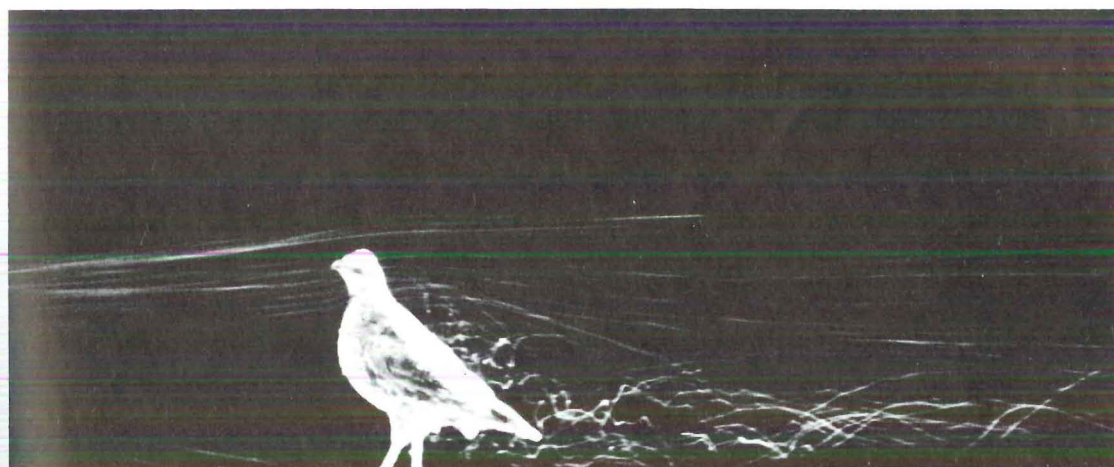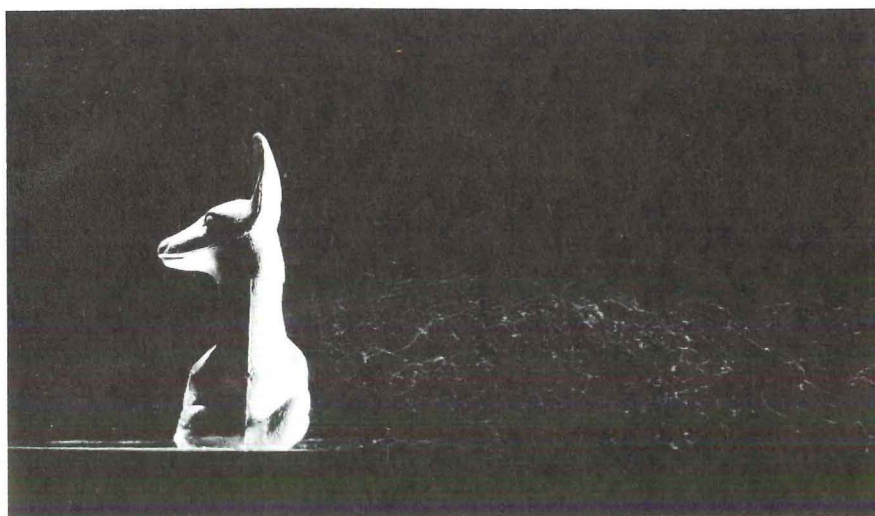T_a = temperature of the air (fluid)

FIGURE 6-15.   Patterns of air flow around (A) a model deer in a bedded posture and (B) a quail in the TEST. Note the turbulent area that develops on the leeward side of the animal.

The equations for calculating convection coefficients for flat plates and cylinders in free and forced convection are shown in Gates (1962). The equation for forced convection h_c across a flat plate is:

$$h_c = 5.73 \times 10^{-3} \sqrt{U/L} \qquad (6\text{-}5)$$

where

h_c = convection coefficient in cal cm^{-2} min^{-1} °C^{-1}
U = velocity in cm sec^{-1}
L = length of the flat plate in cm

The equation expressing h_c for cylinders is:

$$h_c = 6.17 \times 10^{-3} \frac{U^{1/3}}{D^{2/3}} \tag{6-6}$$

where

h_c = convection coefficient in cal cm^{-2} min^{-1} °C^{-1}
U = wind velocity in cm sec^{-1}
D = diameter of the cylinder in cm

The effect of differences in both velocities and diameters is shown in Figure 6-16. There is a higher convection loss per unit area for small cylinders than for large ones. Also, the effect of a change in diameter of smaller cylinders from 2 to 10 cm is several times greater than for a change in the diameter of larger cylinders from 20 to 100 cm. The effect of changes in wind velocity is greatest at the low air speeds; the rate of convection loss for all cylinders rises more steeply in the first $\frac{1}{2}$ to 4 mi hr^{-1}, but then begins to level off.

Two conclusions can be reached from Figure 6-16: (1) small cylinders are more efficient convectors than large ones, and (2) low air velocities have a greater

FIGURE 6-16. Convective heat loss from cylinders of different diameters for each °C temperature difference between the surface of the cylinder and the air.
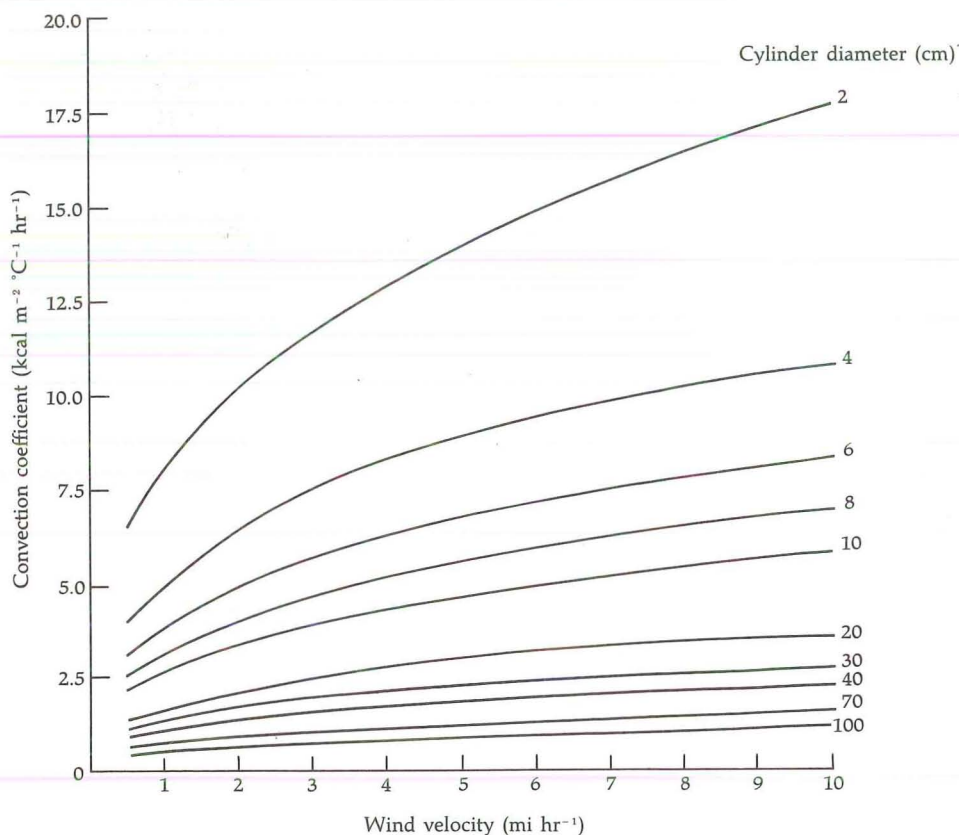
relative effect on convective heat loss than do high air velocities. These conclusions are of ecological significance because animals are, geometrically, collections of imperfect cylinders and cones. Cylindrical hairs are very efficient convectors because of their very small diameter. Thus convective forces can be very effective in removing the radiant heat energy absorbed by the hairs and the heat that is conducted along the shafts of the hairs from the skin surface through the coat.

The convection coefficients expressed in the thermal engineering literature are usually expressed as two-dimensional parameters, dependent on the size of the object and the velocity of the wind. Convection coefficients for animals are n-dimensional, dependent on such factors as size, wind velocity, orientation, hair density, turbulence, radiation absorbed, temperature, and others. These are discussed in Chapter 13.

The relatively greater effect of the lower wind velocities is of ecological interest because so many organisms live in the lower vegetation-filled zone marked by low but highly variable wind velocities owing to the effect of the vegetation on wind flow.

6-6 CONDUCTION

The transfer of heat by conduction results from the exchange of energy when oscillating molecules collide, with a higher rate of exchange during more rapid oscillations. Energy dissipation by conduction is from the higher temperatures resulting from more rapidly oscillating molecules to the lower temperatures. The perfect conductor permits the complete movement of heat energy through the conducting medium, and the perfect insulator prevents all movement of heat energy through the medium. The thermal conductivity (k) of a material is an expression of the rate of heat flow by conduction through the material under a specified set of conditions.

The basic expression used to determine the amount of heat flow by conduction is:

$$Q_k = \frac{kA\,t\,(T_1 - T_2)}{d} \tag{6-7}$$

where:

Q_k = calories of heat transferred by conduction
k = thermal conduction coefficient
A = area
t = time
T_1 = temperature of first surface
T_2 = temperature of second surface
d = distance between the surfaces

Thus the amount of heat flow by conduction depends on the thermal conductivity of the medium, the area over which it is taking place, the temperature gradients, and the depth of the conducting medium. If the thermal conductivity coefficient (k) increases, more heat will be conducted. If either the area or the

time increases, heat flow by conduction increases. If the temperature difference between two points increases, the gradient is steeper and conduction increases. If the depth of the insulating material increases, the amount of heat conducted is reduced.

The conductivity coefficient increases as the temperature of the conductive medium rises. The change is quite small for insulation material. For air, the k value at $-40°C$ is about $\frac{3}{4}$ of the value at $50°C$. There is a linear relationship between the conductivity of air and air temperature, so k can be expressed as:

$$Y = 2.066 + 0.00648X \tag{6-8}$$

where

$Y = k$ in $(\text{kcal m}^{-2}\,\text{hr}^{-1})(°C/\text{cm})^{-1}$
$X = T_a$ in $°C$

This is a useful equation in programing the correction factors when using the economical radiometer (see Appendix 2).

Conduction through the hair layer includes heat flow through the hair shafts themselves and through the air trapped between the hairs. Since air is a better insulator than hair, the important function of hair is the stabilization of the trapped air. This trapped air is a more important thermal barrier than the hair shafts themselves (Herrington 1951). This was demonstrated by Hammel (1953) when he replaced air with freon and determined that the new conductivity coefficient was more dependent on the conductivity of freon than on the hair itself. The same relationship is true for feather surfaces.

6-7 HEAT LOSS BY EVAPORATION

Heat is lost from the surface of a plant or animal by evaporation because energy is absorbed as liquid water is changed to a gaseous state. At $100°C$ the heat of vaporization is 540 kcal per gram, and at $0°C$ it is 595 per gram. There is a linear relationship between air temperature and the heat of vaporization of water (Figure 6-17), which can be expressed by the linear regression equation shown in the figure. Thus if one knows the amount of water evaporated from an organism regardless of the transport mechanism, the amount of energy removed by vaporization can be determined. This has been one of the ways in which Q_e has been measured; subjects are weighed before and after a period of time, and the difference between the first and second weights, minus the weight loss due to urine, feces, and respired CO_2, is the approximate weight of water lost by evaporation.

Evaporative heat loss comes from two sources: evaporation from the skin surface in the form of perspiration from the animal, and evaporation from the lungs and linings of the nasal passages. The relative importance of each source in the total heat loss depends on the characteristics of the animal and the energy characteristics of the atmosphere.

Ecologists have long recognized the importance of water vapor in the distribu-
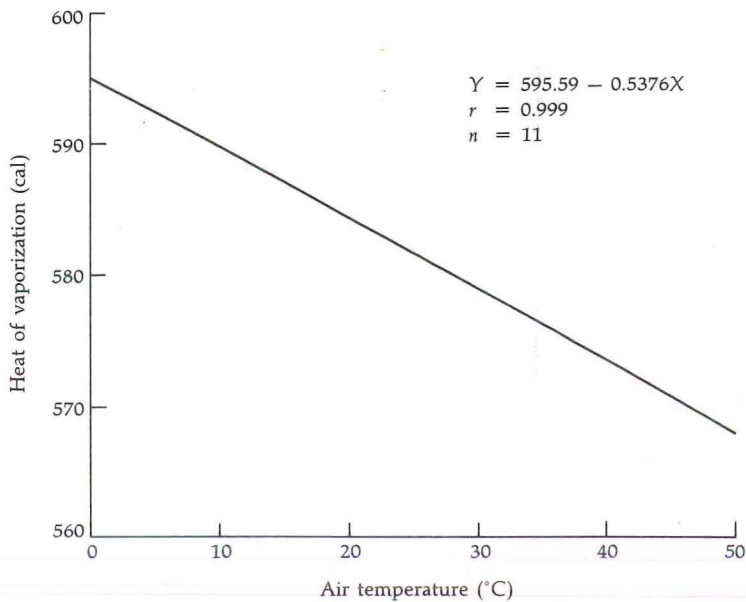
FIGURE 6-17. Linear relationship between air temperature and the heat of vaporization of water.

The graph shows:

$$Y = 595.59 - 0.5376X$$
$$r = 0.999$$
$$n = 11$$

tion and activities of plants and animals. The technique of correlating a biological response with a measured meteorological parameter such as relative humidity has often been used. The next few pages call attention to the concept of heat loss by evaporation, and examples show the errors possible when basic relationships are overlooked.

Relative humidity is the amount of moisture in the air at a particular temperature and atmospheric pressure relative to the moisture content possible under these conditions at saturation. Relative humidity is easily determined (although not necessarily accurately determined), and it is expressed in a well-known unit of measurement—percent. The term relative, however, indicates that it is dependent on another factor, which is temperature. The dependence of relative humidity on temperature results in a "sliding" measurement that changes as either the vapor pressure or the temperature changes. Thus, valid comparisons between relative humidity values can only be made when the air temperatures during measurements are equal.

A common method of determining the relative humidity is by comparing the readings of a dry-bulb and a wet-bulb thermometer. The dry-bulb reading represents the air temperature, and the wet-bulb reading is a reflection of the evaporating power of the air as water evaporates from a wick over the bulb of a thermometer, cooling the bulb. Meteorological tables are used to find the percent relative humidity when the dry-bulb temperature, the wet-bulb temperature, and the difference between the two readings are known (Table 6-3).

TABLE 6-3   A PART OF A METEOROLOGICAL TABLE USED IN DETERMINING
RELATIVE HUMIDITY AND VAPOR PRESSURE

Air Temperature (T_a)	Saturation Pressure	Depression of Wet-bulb Thermometer ($T_a - T_w$)				
		4	5	6	7	8
39	.237	68	60	52	43	37
40	.247	68	61	53	46	38
41	.256	69	62	54	47	40
⋮						
67	.661	80	76	71	67	62
68	.684	81	76	72	67	63
69	.707	81	77	72	68	64

An examination of the characteristics of relative-humidity measurements can lead to several interesting conclusions. Suppose, for example, that the air temperature measured by the dry-bulb thermometer were 68°F and the wet-bulb reading were 62°F. The relative humidity would be 72%, from Table 6-3. If the air temperature were 40°F and the wet-bulb reading 34°F, the relative humidity would be 53%.

The saturation pressure of the air at a temperature of 68°F is .684 inches of mercury, and at an air temperature of 40°F, .247 inches. When the air is saturated, the relative humidity is 100%, of course. When the relative humidity is 72% and the air temperature 68°F, the actual vapor pressure is .684 × .72 = .492 inches, and the vapor-pressure deficit (VPD), or the difference between the actual vapor pressure and the saturation pressure, is .192. At an air temperature of 40°F and a relative humidity of 53%, the vapor pressure is .247 × .53 = .131 inches, and the vapor-pressure deficit is .116 inches. The VPD is a meaningful parameter since it indicates the amount of additional water vapor that can be absorbed by the air up to saturation, and therefore determines the potential amount of evaporative heat loss.

Note in the above example that the relative humidity was 19% higher at 68°F than at 40°F, and the vapor pressure was .361 inches higher. Yet the VPD was also higher: .192 compared with .116 inches! This indicates that the air could hold additional moisture even with a higher relative humidity; the potential for evaporative heat loss would be greater at a higher relative humidity under these conditions.

The usual accuracy of mercury thermometers in sling psychrometers is ±1°F. The actual temperature of the air when the thermometer indicated 68°F could be anywhere from 67° to 69°F. Assuming that the measured temperatures were 68° and 62°F as in the example above, the actual temperature could be 69° and 61°F at one extreme, or 67° and 63°F at the other. The relative humidity values are 64% and 80%, the vapor pressures .452 and .529 inches, and the VPDs are

.255 and .132 in inches for these two examples, respectively. A similar procedure for the 40° and 34°F examples results in 41° and 33°F at one extreme and 39° and 35°F at the other. The relative humidities are 40% and 68%, vapor pressures, .102 and .161, and VPDs are .154 and .076 inches. Note that there is about a two-fold difference in VPDs in the two examples given that can be attributed to *thermometer error alone!*

One final example illustrating the kind of problems associated with the application of relative-humidity data. Suppose that the relative humidity were 50% and air temperatures ranged from 20° to 100°F. Air-temperature increments, vapor pressures, and VPDs representing the cooling power of the atmosphere at different air temperatures are shown in Figure 6-18. Note that it is distinctly nonlinear although the relative humidity is a constant 50% in this example.

The foregoing examples indicate the need for using meaningful parameters in studying the relationship between an animal and its environment. Relative-humidity data are inadequate for the analyses of evaporative heat loss from animals. Allen et al. (1964) found that the moisture content of cattle coats was not related to the measured relative humidity, but it was related to the vapor

FIGURE 6-18.   Vapor pressure deficits at different air temperatures with a *constant* relative humidity of 50%.
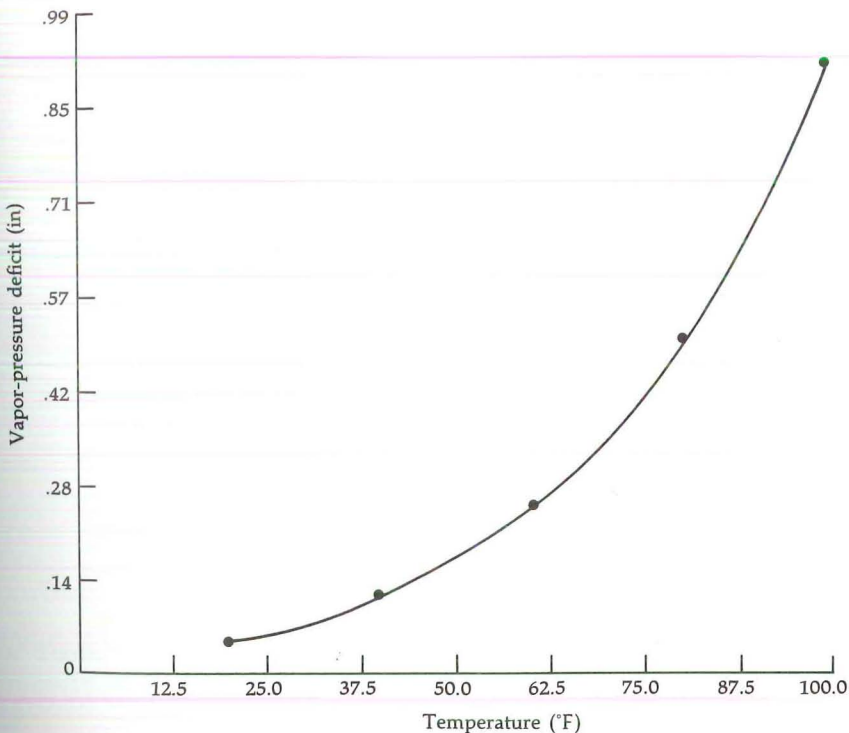
pressure of the air. Relative humidity is only an index, and its use alone may result in fallacious conclusions about evaporation losses.

The use of VPDs in ecological analyses is facilitated by the use of an equation for the calculation of VPD from inputs of T_a in relative humidity (%) (Table 6-4). The nonlinearity of this relationship is accounted for by the log transformation. The use of equations for these kinds of calculations facilitates the evaluation of the importance of one environmental factor in relation to others under consideration over a wide range of values. If the VPD were found to be important, the accuracy of the equation in Table 6-4 may need to be improved.

At low temperatures, the amount of heat lost by evaporation appears to be fairly constant. Evaporative heat loss by sheep was constant until ambient temperatures reached 30°C (Blaxter et al. 1959). This is reasonable since surface-water loss is slight when the surface of the animal is cool. Also, the vapor pressure of the air is low at colder temperatures, so the VPD cannot be very large. Wind, however, constantly brings new air over the source of evaporating water, so even air with a low VPD may still not become saturated. Thus heat loss by evaporation can continue even with low VPDs when there is wind.

The calculation of heat loss by evaporation is very complex because of the interaction between thermal factors, mass transport of water vapor and air, and surface characteristics. Sturkie (1965) discusses evaporative heat loss from birds,

TABLE 6-4   TABULATED AND CALCULATED SATURATION PRESSURES

T_a	Tabular Saturation Pressure (mm of Hg)*	Calculated Saturation Pressure†	Deviation	% Deviation
0	4.579	4.855	+0.276	6.0
5	6.543	6.619	+0.076	1.2
10	9.209	9.025	−0.184	2.0
15	12.788	12.305	−0.483	3.8
20	17.535	16.777	−0.758	4.3
25	23.756	22.874	−0.882	3.7
30	31.824	31.187	−0.637	2.0
35	42.175	42.521	+0.346	0.8
40	55.324	57.974	+2.650	4.8

*Handbook of Chemistry and Physics.
†The vapor pressure can be expressed by the following equation:

$$\log VP = (1.580 + 0.062\ T_a); \quad r = 0.999; \quad n = 9$$

The vapor-pressure deficit can then be calculated by the following equation:

$$VPD = e^{(1.580\ +\ 0.062 T_a)} \left(\frac{100\ -\ \%R.H.}{100} \right)$$

and others have considered evaporation losses from plants. One thing is clear to anyone who has considered this question—relative humidity is an entirely inadequate parameter for ecological considerations, and continued presentation of relative-humidity data alone is of no value.

6-8 CONCLUSION

The apparent distribution of matter and energy in relation to physical and biological objects is complex, especially because of the changing distributions due to daily and seasonal cycles such as daylength and seasons, local variations due to weather, long-term changes due to geological aging, and the mobility of organisms that traverse energy flux and different types of matter as they go about daily activities. There is a basic simplicity to the distribution, however, and large quantities of tabular information can often be reduced to mathematical equations that can be successfully used to analyze relationships between physical and biological factors if the model or system is analyzed in a functional way.

Part 2 has included descriptions of simple models that illustrate the manner in which analytical ecology is approached. The emphasis in this chapter on the thermal characteristics of weather is because of the tendency of ecologists merely to compare weather data with biological data, when in reality there is thermal interaction. This interaction cannot be studied in an ecologically meaningful way until the metabolic, nutritive, and behavioral characteristics of organisms are understood. Parts 3 and 4 include considerations of physiology and behavior, with an emphasis on wild ruminants. The principles are applicable to any species, and students of analytical ecology are urged to develop equations expressing physiological and behavioral characteristics of other species. This will result in new information on a variety of species.

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