13

THERMAL ENERGY EXCHANGE
BETWEEN ORGANISM
AND ENVIRONMENT

13-1 THERMAL ENERGY EXCHANGE

The effects of weather are manifested in an organism-environment relationship through the medium of thermal or heat exchange. Meteorological parameters alone may be quite meaningless when used in interpreting animal responses because weather instruments do not respond to the thermal regime of the atmosphere in the same way that a living organism does. Further, weather instruments are often placed in standard weather shelters at standard heights so that as many variables as possible are eliminated. A living organism, however, is exposed to changing weather conditions, and it also has its own physiological and behavioral variables. Knowledge of the basic principles of heat exchange enables the biologist to understand the functional relationships between weather and the living organism.

An organism is *coupled* to energy-exchange processes by certain specific properties of its own (Gates 1963). The amount of heat exchange by radiation, convection, conduction, or evaporation depends on the thermal characteristics of the atmosphere and substrate, such as soil, rock, or snow, and the thermal characteristics of an organism. If a surface is highly reflective to radiant energy, then there can be little thermal effect from radiation. A cylinder with a very small diameter is a very efficient convector and slight air movement can result in a large amount of heat loss. Conversely, a large cylinder is a poor convector. An object covered with a layer of good insulation loses little heat by conduction, and an object with no water or other fluid that can be vaporized can have no heat loss by evaporation.

The thermal characteristics of an organism are related to its physiological and behavioral characteristics also, and these may change drastically in a short period of time. A deer, for example, may be bedded quietly until frightened, when it literally leaves its bed on the run! This results in very abrupt changes in the thermal regime.

It has been traditional to categorize animals as either homeothermic or poikilothermic, but the distinction between the two is not entirely clear. Reptiles can regulate their body temperatures somewhat by behavioral thermoregulation, including changes in activity, location, and posture.

Mammals do not have the same body temperature throughout their entire bodies. Deep body temperature is quite constant, with the temperatures of appendages more closely coupled to the external thermal environment. Hibernating mammals regulate their body temperatures by increasing heat production when their body temperatures approach the freezing point. They are in a sense homeothermic, but at a lower set point.

13-2   THE CONCEPT OF HOMEOTHERMY

Warm-blooded or homeothermic animals are usually described as animals that maintain a constant body temperature. This very simple idea is often presented to students in elementary grades, and it is commonly said that the body temperature of humans is 98.6°F. All humans do not have the same body temperature though, and all parts of the human body are not at the same temperature.

Careful consideration of the basic concept of homeothermy leads to a conclusion that is much more basic than the simple statement that the body temperature remains "constant." Heat energy is produced when food is "burned," and heat is lost to the environment when the environment is colder than the animal. Homeothermic animals regulate the balance between heat production and heat loss. The *effect* of this balance is a relatively constant body-core temperature.

The actual heat exchange between a homeothermic animal and its environment is very complex. The concept is simple, however, and can be illustrated by the example of a heated home in the winter (Figure 13-1). Fuel is burned in the furnace, and the heat energy is distributed throughout the house by water or steam pipes or by air ducts. The amount of heat energy distributed throughout the house is controlled by a thermostat that can be set at a desired temperature.

The fuel in the furnace (oil, gas, coal, or wood) is a source of energy like the food eaten by an animal. The water pipes, steam pipes, or air ducts are like the blood vessels. The thermostat can be compared to the hypothalamus in an animal—a part of the brain that regulates heat production. If the weather gets colder, the fire in the furnace will burn longer in order to maintain a balance between the amount of heat energy released from the furnace and the amount of heat lost from the house. The net result is the maintenance of a constant house temperature. The Astrodome in Houston, Texas, operates in a similar manner, with air conditioning to keep it cool in the summer and furnaces to keep it warm in the winter. There are instruments or "nerve endings" on the outside surface
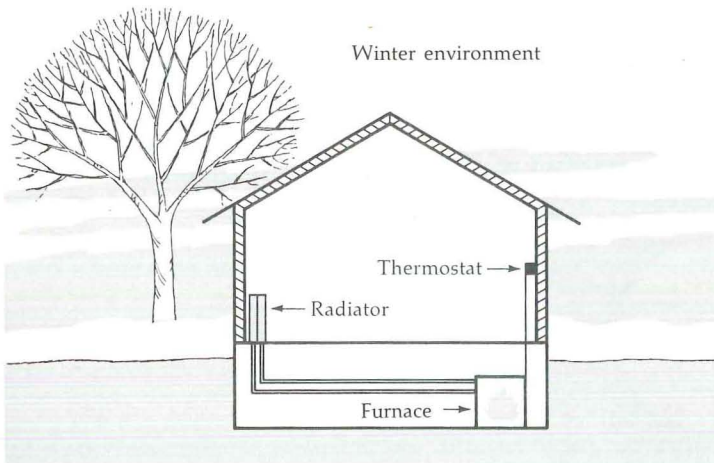
FIGURE 13-1. A heated home is like a homeothermic animal; a balance between the heat energy produced in the heat source (furnace) and the heat energy lost to the heat sink (the winter environment) is regulated by a thermostat so that the house temperature remains quite constant.

of the Astrodome that perceive the amount of energy striking it from the sun, just as a person feels heat energy on the skin surface in bright sunlight!

REGIONS OF THERMAL EXCHANGE.   The exchange of heat between animal and environment occurs in three distinct regions, including the internal thermal region, the boundary region, and the external thermal region. The external thermal region includes both the atmosphere and the substrate (Figure 13-2). The internal thermal region includes all of the body tissue except the hair. Heat flow through body tissue is primarily by conduction and convection, with additional heat exchange by evaporation in the respiratory tract.

The rate of conduction in this region depends on the thermal conductivity of the different kinds of body tissue, including muscle, fat, bones, and other tissue. The circulation of blood results in the distribution of heat within the body by conduction and convection. The sites of active metabolism may have an excess of heat energy, which can be removed by the flow of blood and dissipated in areas in which the body tissue is cooler. Thus the circulatory system is a *thermal transport system* as well as an oxygen and carbon dioxide transport system.

The boundary region is a thermally active region in which the influence of the animal's surface is exerted, both physically and thermally, on the external thermal region. Temperature differences between the internal thermal region of animals and the external thermal region (the atmosphere) often exist, resulting in temperature gradients that characterize the boundary layer. Further, the boundary region surrounding birds and mammals includes the feather-air and hair-air interfaces, respectively.
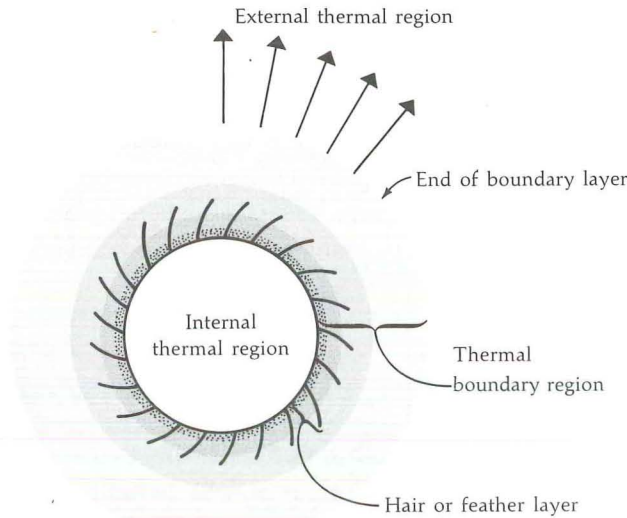
FIGURE 13-2.   The three regions of heat exchange between animal and environment: internal thermal region, boundary region, and external thermal region.

The hair-air interface is a fibrous and porous medium with a density gradient from the base to the tips of the hairs, while a feather-air interface has a density gradient and a considerable amount of lateral overlap (Figure 13-3). These physical characteristics result in a very complex heat transfer that is made even more complex by the pliability of the hair or feather coat. Movement of the hairs or feathers increases the rate of heat transfer because it disturbs the hair-air or feather-air geometry.

The relative importance of each mode of heat transfer varies across the interface layer. Conduction is the most important mode at the base of the hair because the hairs are tightly packed together and there is little air movement. Heat is conducted along the shafts of the hairs (or feathers) and through the air that is trapped between them. The space between the hairs in the outer portions of the hair-air interface is greater and the hair shafts are more exposed to the environment. Thus there is radiation exchange between the surfaces of the hair shafts and the surroundings. The decreased density of the hair permits a larger amount of air movement so convection processes accelerate. Each hair functions as a little convection cylinder exposed to both free and forced convection, and the proportion of free and forced convection is dependent on the air motion at the site of convection and the amount of penetration by the wind. The overlapping feathers function in a similar manner, with some modifications due to differences in physical morphology.
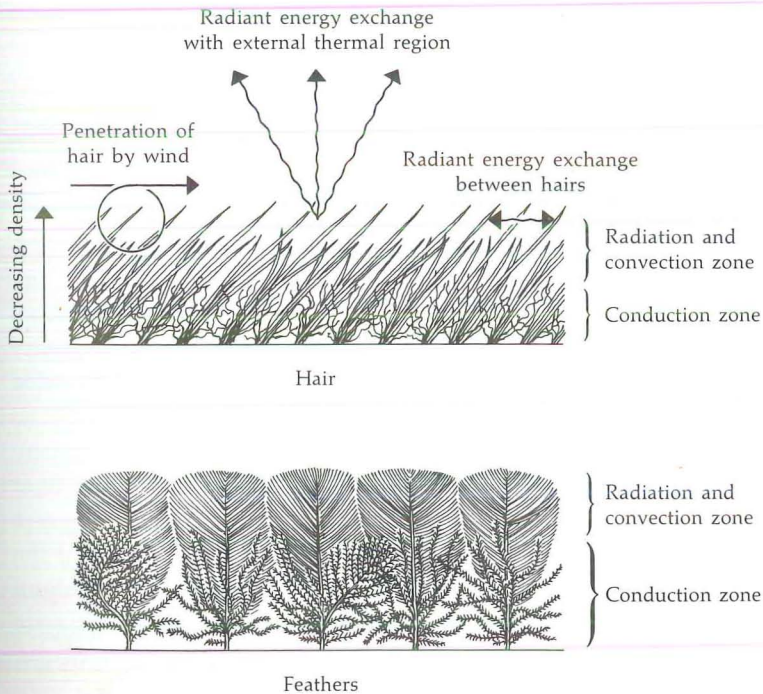
Evaporative heat exchange through the interface results if energy is involved in the conversion of secretions of the skin or of rain or snow from a liquid to a gaseous phase. The rate at which this change of phase occurs is dependent on

the movement of water molecules in the interface. A very dense hair layer will trap water molecules at the skin surface and will also prevent the penetration of rain or melted snow. The oily characteristic of an animal's coat further enhances its protective characteristics. The destruction of normal feather structure by oil on the surface of ducks destroys its insulative and waterproof characteristics, resulting in a high rate of heat flow through the feather-air interface.

ANALYSES OF HOMEOTHERMIC RELATIONSHIPS.   A basic concept that emerges from the consideration of all of the thermal relationships between animal and environment is that the thermal exchange of an animal is centered on the heat flow through the boundary region. This region, including hair or feather insulation, is a barrier to both heat absorption and heat dissipation. If the functional thermal characteristics of the boundary region are known, then the calculated heat flow through that layer will be in balance with the heat production of the animal and with the heat loss from its surface, with the additional consideration of the heat lost by respiratory evaporation.

There are two approaches to the study of homeothermy. One is to measure the heat production of an animal in a chamber, which can be assumed to be equal to the heat loss as long as the body temperature remains stable. The other is

FIGURE 13-3.   A schematic representation of the structural characteristics of hair and feathers that determine the types of heat transfer through the hair or feather layer.

Radiant energy exchange with external thermal region

Penetration of hair by wind

Decreasing density

Radiant energy exchange between hairs

Radiation and convection zone

Conduction zone

Hair

Radiation and convection zone

Conduction zone

Feathers

to measure the heat loss, which can be assumed to be equal to the heat production if body temperature remains stable.

The use of heat-production measurements as analogs to heat loss is valid, but the means by which heat is lost are usually not considered in this type of analysis. An animal held in a refrigerated metabolism chamber exhibits an increase in heat production as ambient conditions in the chamber become colder. This provides very useful information on the metabolic potential of the animal, but the chamber temperature does not represent outdoor conditions in which so many other thermal factors are present. The use of a mask on an animal held outdoors provides a more realistic exposure of the animal to natural weather conditions, but the limitations imposed by the mask prevent the animal from exhibiting normal behavioral responses.

The calculation of heat loss is very complex owing to the complicated geometry of the animal and the very labile nature of the thermal energy regime that is commonly referred to as weather. The heat loss must be equivalent to the heat production except for transient fluctuations over short periods of time.

The synthesis of heat-production and heat-loss measurements into a single unified concept of heat exchange is the most logical approach to the analysis of the energy requirements of a free-ranging animal. The animal and its thermal environment are a thermal system, a homeostatic one; and analyses of the relationships between the two should include the recognition of every system component.

13-3   MEASUREMENT OF THERMAL PARAMETERS

CONDUCTION COEFFICIENTS.   A thermal conduction coefficient (k) is an expression of the rate of heat flow through an insulating medium per unit depth for each degree of difference in temperature. A perfect insulator would have a k value of zero. The conduction coefficient is a necessary parameter for the calculation of heat flow by conduction. The thermal conductivity coefficients of wild ruminants reported in the literature are shown in Table 13-1.

Conduction coefficients cannot be expressed as single values for each species, however, since the density of the hair or feather layer, the compression and wetness of the hair or feathers, inclination of the shafts, air temperature, radiation, and wind all affect the conductivity. Hammel (1953) has measured the conductivity of summer and winter coats of several mammals, and the greater insulation value of the winter coat seems to be primarily a function of depth.

The rate of heat flow through fibrous material is high when the fiber density (ratio of fiber material to air) is low. It decreases as the density of the fiber increases up to a certain point, and it increases again as the density increases further. Convection and radiation exchange are also important, especially at the lower densities, increasing the total heat flow. Berry and Shanklin (1961) found that cattle with denser hair coats had a higher heat transfer; the hair shafts are better conductors than the air between the hairs. There is less air space in denser hair and in compressed hair, and the amount of air in the hair layer is a very important characteristic affecting conductivity (Hammel 1953).

TABLE 13-1 THE INSULATION VALUES OF FURS

Pelt	Thickness of Fur (cm)	Conductivity per Cm of Hair Layer ($kcal\ m^{-2}\ hr^{-1}\ ^{\circ}C^{-1}$)	Total Conduction
Virginia deer no. 1* (early fall, fresh pelt)	1.7	3.32, 3.30	1.95, 1.94
Caribou no. 1*		3.29, (3.30)	1.94, 1.94
(fresh winter pelt) (air 7°)	2.5	2.88	1.15
Caribou parka* (air 24°)	1.5	3.26	2.17
Caribou† (winter)	3.28	3.81	1.18
Caribou† (summer)	1.19	3.13	2.66
Caribou† (thin summer)	0.74	3.06	4.17
Deer† (winter)	2.39	3.06	1.28

* Data from Hammel 1953.
† Data from Moote 1955.

The compression of fibrous insulation such as hair or feathers is an important factor in determining the rate of heat loss by conduction from the animal. A bedded deer, for example, compresses the hair on its legs and trunk. The snow under the deer melts as heat is conducted from the body through the compressed hair. Direct measurements of heat flux under deer indicate that this heat loss is important when considering the energy requirements of the deer (Moen, unpublished data).

The amount of moisture in the coat has a marked effect on the rate of heat flow through the conduction zone in the hair layer. This was indicated by the large increase in the metabolism of infant caribou when their coats were wet (see Table 7-7).

The inclination of the hair or feather shafts affects the rate of conduction through these media. The lowest rate of conduction occurs when the fibers are parallel to the plane of the insulation and perpendicular to the mean direction of heat flow, and the highest when the fibers are perpendicular to the plane of the insulation and parallel to the direction of heat flow (Figure 13-4).

Hair in normal lie falls between the parallel and perpendicular extremes. It has its maximum insulation per unit depth when in normal inclination. Piloerection results in a decrease in the insulation value of the fur per unit depth, but Hammel (1953) has data that indicate that the increase in depth compensates for the change in hair inclination. The total insulation of the erect fur was slightly greater than the total insulation of fur in normal position. These relationships have also been observed by Berry and Shanklin (1961) for cattle. The inclination

Direction of heat flow.

A. Fibers parallel to plane of insulation
   and perpendicular to direction of heat flow.

B. Fibers perpendicular to plane of insulation
   and parallel to direction of heat flow

C. Normal inclination of deer hair

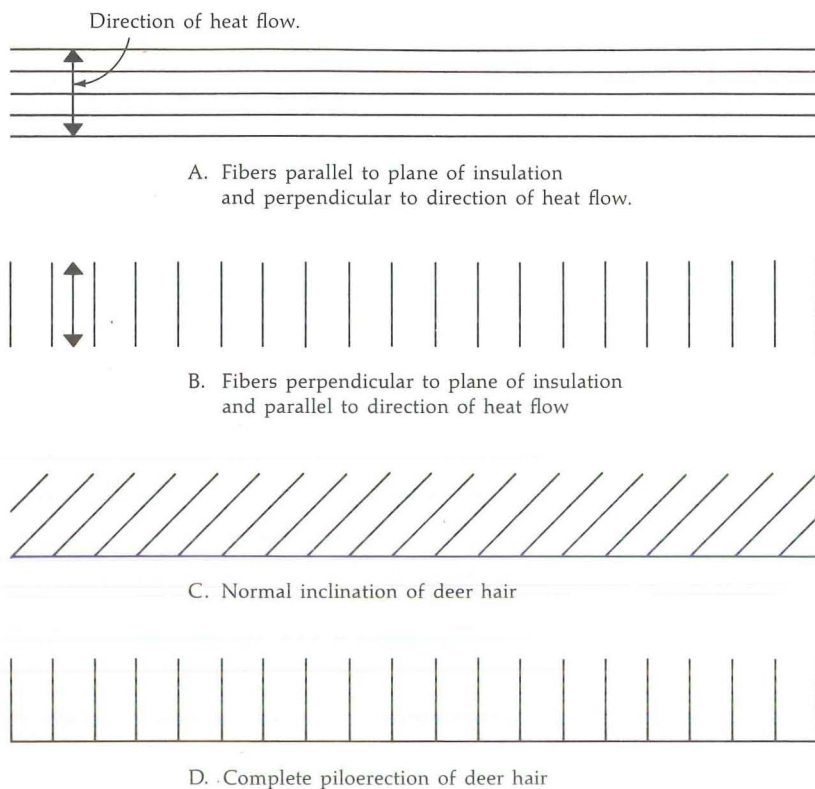D. Complete piloerection of deer hair

FIGURE 13-4. Heat flow in relation to the inclination of the fibers (arrows indicate direction of heat flow): A is the best insulator, B the poorest. Normal inclination of deer hair is between A and B.

of the hair had more influence on hair-coat conductivity than other measured parameters. Increasing depth-to-length ratios increased the conduction of heat, but the increase in hair depth caused a decline in the conduction loss through the entire length of the hair coat.

The temperature of the air around the fur affects the conduction rate through the fur layer itself. The experiments of Hammel (1953) show that the insulation of dog, hare, and fox pelts was greater in colder temperatures. This is to be expected since the conductivity of air has a major influence on conduction through the hair-air interface, and air has a lower thermal conductivity at lower temperatures. This was expressed in equation (6-8).

The rate of heat flow through the hair-air interface is affected by both the velocity of the wind and the angle at which the wind strikes the hair or feather surface. The effective angle is not a single value determined from the mean wind direction, but is an extremely variable parameter that is dependent on the geometry of the animal in relation to the mean wind direction and on the turbulent wind-flow characteristics at the animal's surface.

The insulation value of fibrous material decreases as the wind velocity increases and the angle at which the wind strikes the surface increases from zero or parallel

flow. Experiments on merino sheep fleece show this effect (Allen et al. 1964), and higher conduction or lower insulation values for rabbit fur exposed to higher wind velocities were reported by Tregear (1965). Tracy (1972) discusses conductivity through an animal's hair coat, pointing out that wind speed is an important consideration in determining the overall conductance of an animal. A similar conclusion has been reached for white-tailed deer also (Stevens 1972) and for sharp-tailed grouse (Evans 1971).

TEMPERATURE-PROFILE MEASUREMENTS. Measurements of the thermal characteristics of the hair-air layer from the trunks of white-tailed deer have been completed in the Thermal Environment Simulation Tunnel (TEST) (Figure 13-5) at the BioThermal Laboratory. Simulations (Figure 13-6) are used in the TEST to reduce the experimental conditions to a physical system devoid of biological variability. This permits an analysis of the mechanisms of heat flow according to the basic principles of thermal engineering. These measurements are then compared with results of similar measurements of live deer with their biological variability superimposed on the effects of uncontrolled weather factors, including wind, radiation, and temperature.

The validity of results from a simulation is often questioned. My own research at the University of Minnesota indicated agreement between measurements of simulations and those of live deer, and this has been confirmed in current experiments. The agreement appears to result from the dominant effect of the hair layer

FIGURE 13-5. The TEST is used to measure the thermal characteristics of animal simulators exposed to controlled wind and radiation conditions.


0   5 Feet
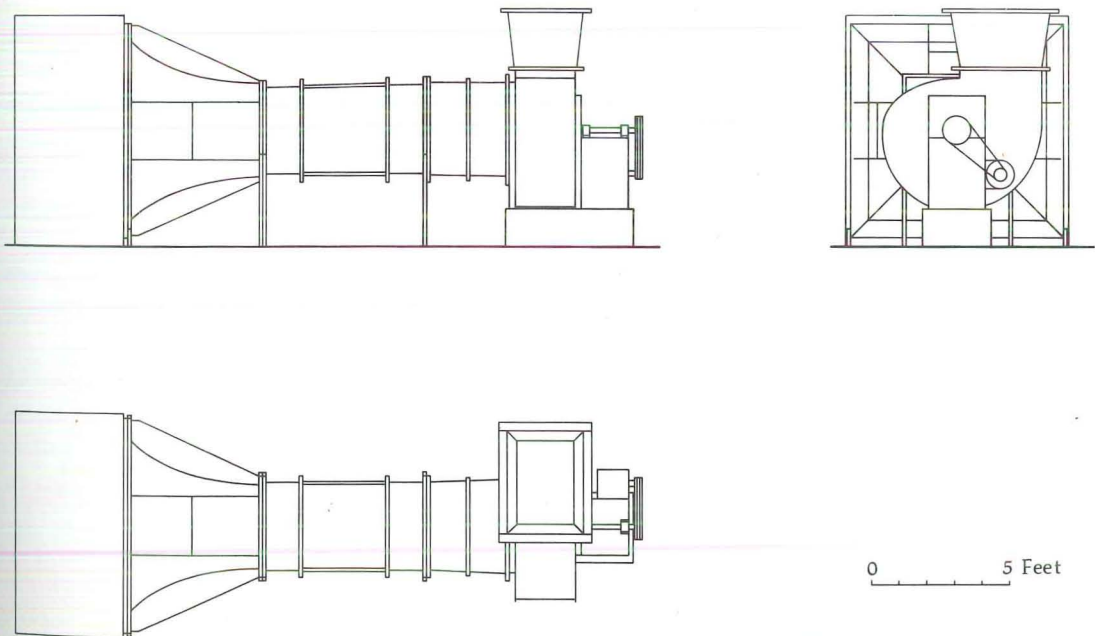
as a thermal barrier. This barrier is primarily a physical one and is therefore subject to the physical laws of heat transfer with little regulation by the animal of the thermal characteristics of the hair layer itself. Further, simulations are used to understand the mechanisms of heat flow under controlled conditions, and not necessarily to provide actual data that are numerically equal to values for live animals.

TEMPERATURE PROFILES IN FREE CONVECTION.   The first consideration of the thermal characteristics of the deer simulator is the nature of the temperature profile under stable radiation conditions and no wind (Figure 13-7). Temperature measurements with thermocouples at different depths indicate that the boundary layer of temperatures extends from the skin surface to about 4 cm. The temperature field within this 4-cm zone is a function of the thermal characteristics of the simulator, and this effect extends beyond the hair itself. At lower air temperatures the gradient is steeper, at higher temperatures the gradient is less steep, and at 38°C the gradient line would be vertical. The very systematic shape to these curves indicates that the relationship between air temperature and the temperature profile is a predictable one.

TEMPERATURE PROFILES IN FORCED CONVECTION.   Wind has an effect on the distribution of temperatures in the boundary region. A wind velocity of 6 mi hr^{-1} results

FIGURE 13-6.   A schematic drawing of a deer simulator used in the TEST.
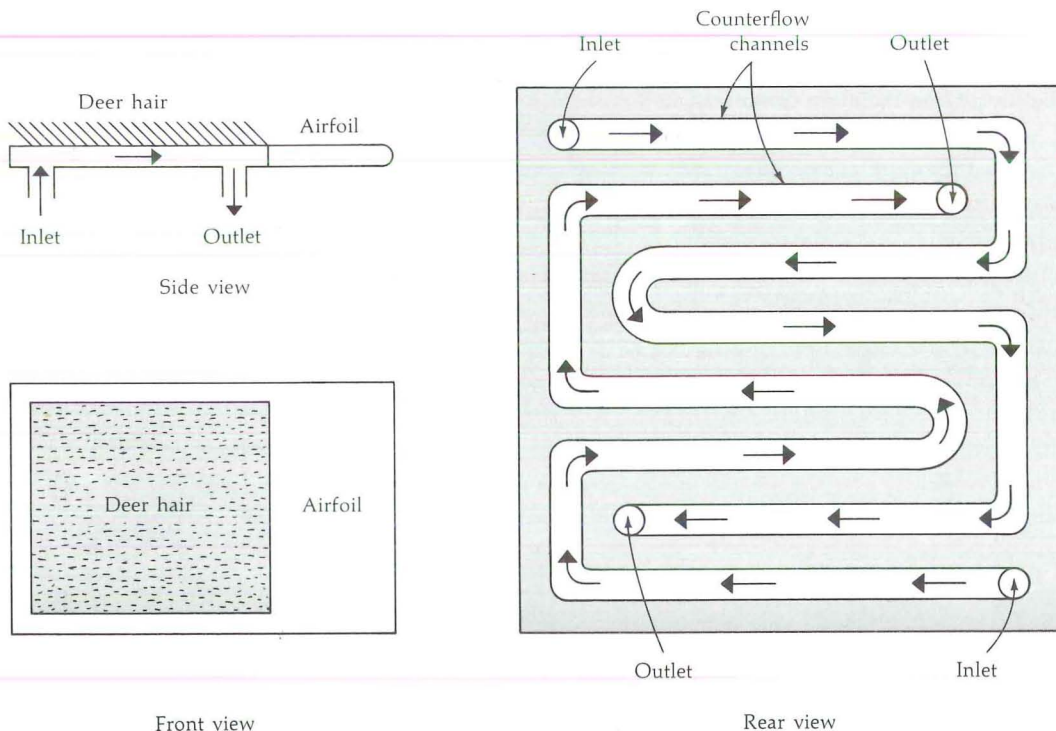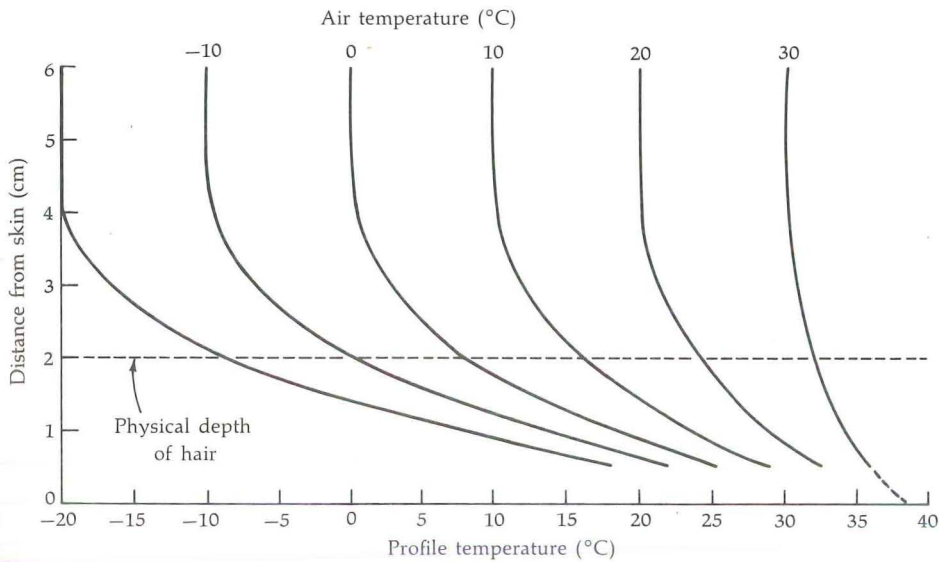
FIGURE 13-7. The temperature profile of a white-tailed deer simulator in free convection in the TEST. (Data from Stevens 1972.)

in a compression of the temperature field in deer hair to a depth of about 3 cm (Figure 13-8). The effect of wind on the compression of the temperature field at an air temperature of $+20°C$ is less than at $-20°C$. As velocities increase, the profile is compressed more (Figure 13-9).

A distinctly nonlinear effect of wind on the temperature profile and surface temperature of deer hair has been observed in our experiments on white-tailed deer and is also reported by Tregear (1965) for rabbits, horses, and pigs. The lower wind velocities have a proportionately greater effect than high velocities, and the temperature depression in the boundary layer is also related to the density of the hair. The nonlinear effects of velocity on the temperature field in deer hair are evident in Figure 13-9. At an air temperature of $0°C$ an increase in wind velocity from 0 to 6 mi hr^{-1} results in a $3.8°C$ decrease in surface temperature (from point A to point C), but an increase from 6 to 14 mi hr^{-1} causes an additional decrease in surface temperature of only $1.5°C$ (from point C to point E).

Simulator measurements of sharp-tailed grouse show a pattern very similar to that for deer (Figure 13-10). The temperature profile is steepest in the feather layer, with the end of the boundary region at about 7 cm.

Figures 13-7 through 13-10 show the characteristics of the temperature profile of the simulators when the wall infrared temperatures in the experimental tunnels are in equilibrium with air temperature. This is similar to the thermal conditions in the field when an animal is under heavy coniferous cover or the sky is overcast at night.

TEMPERATURE PROFILES UNDER RADIANT ENERGY LOADS. Absorbed radiant energy is important in the maintenance of homeothermy. This energy becomes a part

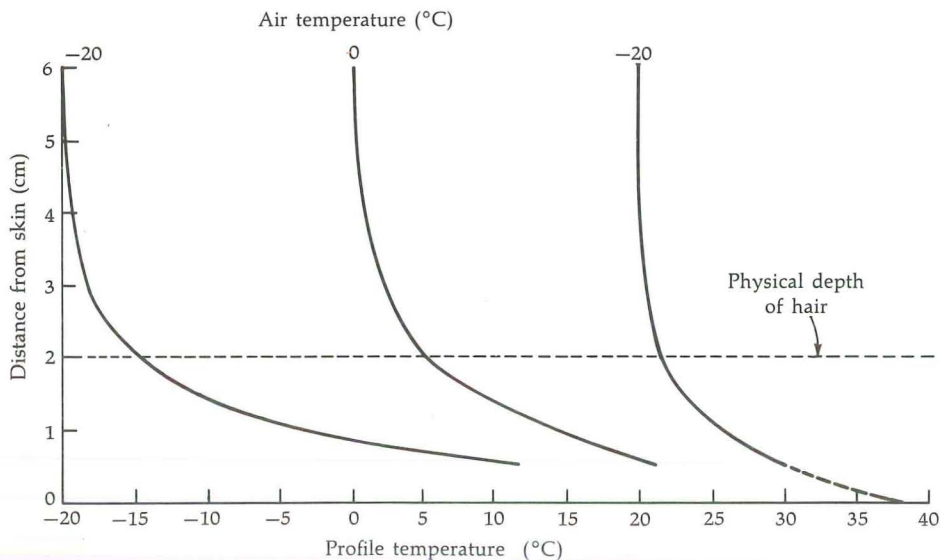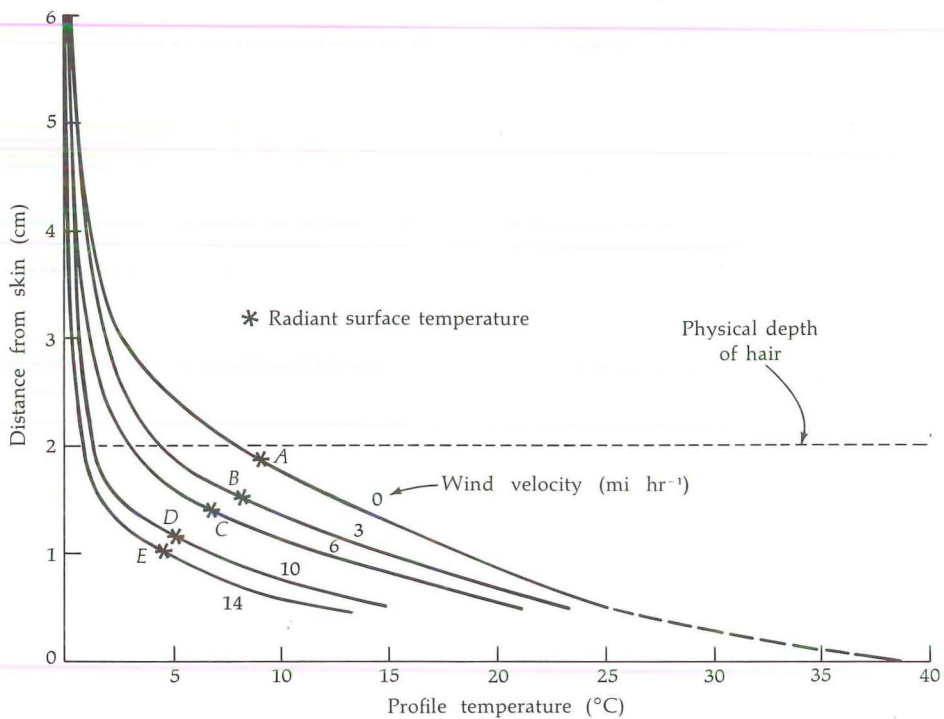FIGURE 13-8. The temperature profile of a white-tailed deer simulator exposed to a wind velocity of 6 mi hr^{-1} in the TEST. (Data from Stevens 1972.)

FIGURE 13-9. Temperature gradients in the thermal boundary region of a deer simulator in an air temperature of 0°C. *A, B, C, D*, and *E* indicate radiant surface temperature. (Data from Stevens and Moen 1970.)
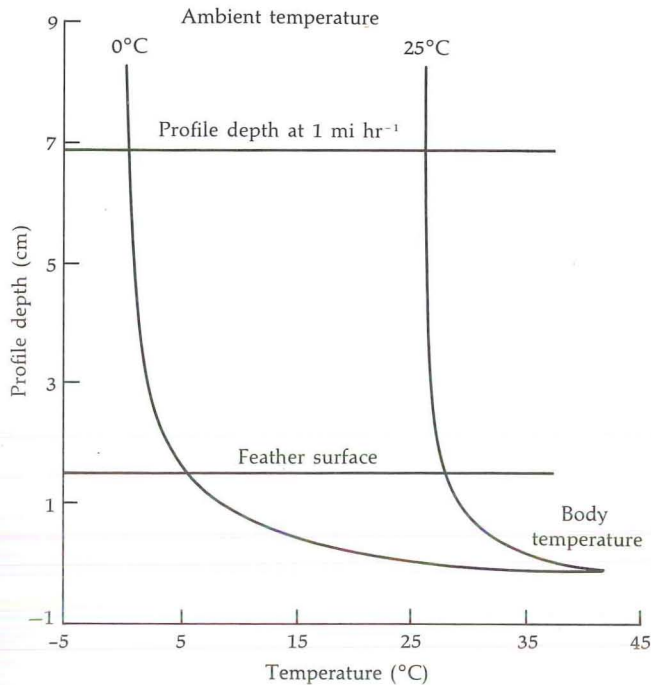
FIGURE 13-10.   The thermal profile of sharp-tailed grouse feathers exposed to a wind velocity of 1 mi hr⁻¹. (From Evans 1971.)

of the thermal regime of the animal, and it can be dissipated by any one of the four modes of heat transfer. 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 were shown in Figure 6-3. White coats absorb less solar energy and reflect more; black coats absorb the most solar energy. The greatest amount of energy is absorbed when the solar radiation strikes perpendicular to the surface, with no absorption when the rays are parallel to the surface. Since animals are not plane surfaces but have a rather complicated geometry, the absorption characteristics of a whole animal include all angles from 0 to 90 degrees. Inclination of the hair, the smoothness or curliness of the coat, and seasonal changes in the characteristics of the coat change the absorptivity by less than 2%. The distribution of solar radiation on the surface of an animal is called the solar-radiation profile, which was discussed in Chapter 6.

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 usually a satisfactory approximation; the error in using this approximation increases as the temperature difference between two surfaces exchanging radiant heat increases. The error is

usually small in the range of temperatures experienced by animals in natural habitats.

Experiments in the TEST with an infrared lamp as a radiant energy source of 0.5 cal cm^{-2} min^{-1} show that at an air temperature of 20°C, the temperature profile in deer hair has an inversion at wind velocities of 0 and 1 mi hr^{-1} (Figure 13-11). As wind velocity increases, the effect of radiation on the temperature profile is reduced. Radiant energy absorbed in the outer portions of the hair layer is removed by convection so that the net effect on the animal's thermal regime may be considerably less than the measurements of radiation flux alone would indicate. This convection process is very efficient at the hair surface since each hair acts as a tiny convection cylinder and all of the hairs together expose a very large surface area to the wind.

The same general pattern in the temperature profile is observed when the air temperature is −20°C, except that the inversions do not occur at the low wind velocities because the relative effect of the radiation is less at low air temperatures. At 14 mi hr^{-1} the effect of radiation is negligible; the profiles are essentially the same as those in Figures 13-7 through 13-10.

13-4   RADIANT SURFACE TEMPERATURE RELATED TO AIR TEMPERATURE

There is a predictable relationship between the radiant temperature (T_r) of an animal and the air temperature if radiation and convection conditions are held constant. The difference between the radiant temperature and air temperature is greatest when the air is cold and the wind velocity high. This was illustrated for both deer and grouse in Figures 6-8, 6-9, and 6-10.

FIGURE 13-11.   The temperature profile of a white-tailed deer simulator at two air temperatures and five wind velocities when exposed to thermal radiation in the TEST. (Data from Stevens 1972.)
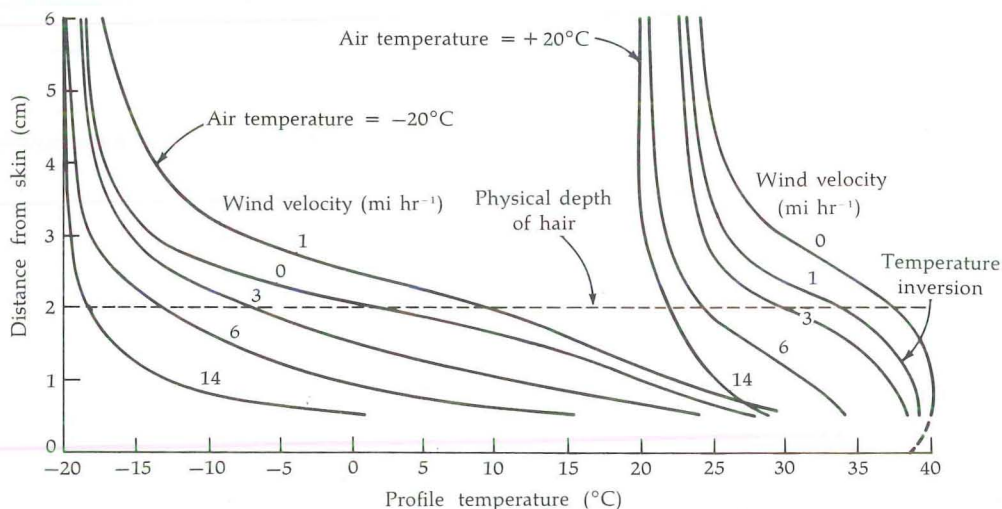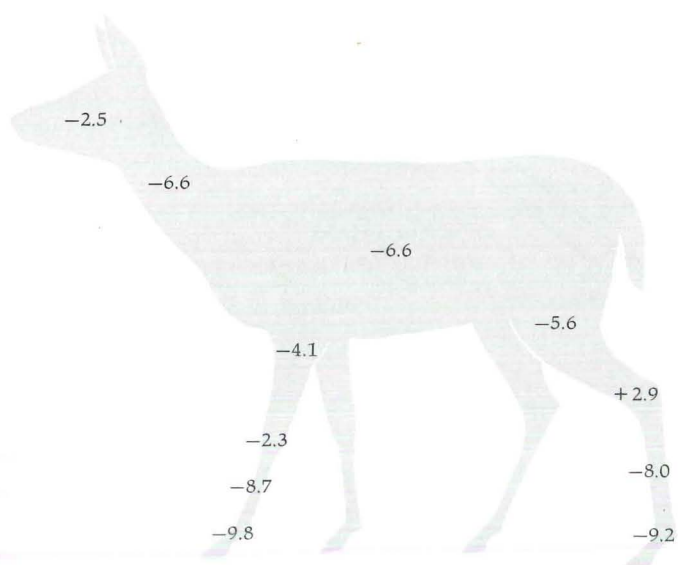
FIGURE 13-12.   Radiant temperatures (in °C) on eleven body parts of white-tailed deer exposed to an air temperature of −20°C. (From Stevens 1972.)

Radiant temperature measurements taken at fifty-one points on deer have been completed throughout two winters at the BioThermal Laboratory. A "thermal profile" composed of regression equations expressing the radiant surface temperature in relation to air temperature has been calculated (see Appendix 4). An illustration of radiant temperature distribution on eleven body parts at an air temperature of −20°C is shown in Figure 13-12. Note that at an air temperature of −20°C the radiant surface temperature of the deer varied from a high of 2.9°C on the hock to a low of −9.8°C on the lower part of the front leg. These temperature differences can be explained by the anatomy and physiology of the circulatory system, differences in hair depth on different parts of the body, wind flow, and other variables.

Maximum and minimum trunk temperatures of deer during each measurement period are expressed with regression equations and compared with the regression equation for a simulator in Figure 13-13. A slightly greater variability in the results for a live deer (compare the r values) is expected since more biological factors are involved, and also the wind conditions in the outdoor pen are more variable than those in the TEST.

Radiant temperature measurements on sharp-tailed grouse show a similar general pattern, with much less variability over their surfaces because of their simplified geometry. The data points and correlation coefficient for the sharp-tailed grouse tests at 1 mi hr^{-1} are shown in Figure 13-14.

A final generalization on the effect of wind and radiation on the thermal boundary region is that the effect of radiant energy is greatest at high air temperatures and low wind velocities and least at low temperatures and high wind
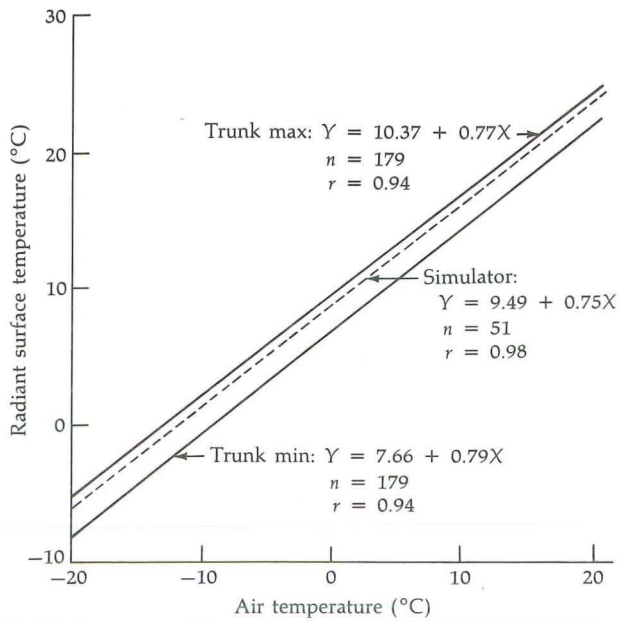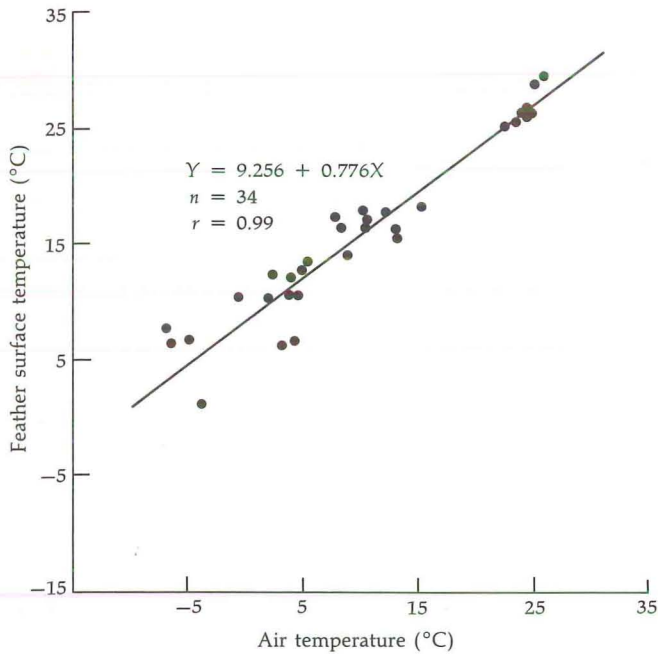
FIGURE 13-13. Radiant surface temperature in relation to air temperature for a flat-fur simulator and the body trunk of live deer in free convection. Maximum and minimum values are presented for the deer. (From Stevens 1972.)

FIGURE 13-14. Effect of air temperature on feather surface temperature of sharp-tailed grouse at a wind velocity of 1 mi hr^{-1}. (From Evans 1971.)

velocities. This suggests that the reduction of wind velocities is one of the most important benefits of cover in the winter. The thermal benefits due to different levels of radiation from different types of cover can be evaluated only if free or forced convection is considered also.

13-5 THE CONCEPT OF THERMAL DEPTH

One concept that has emerged from the experiments in the TEST is that of thermal depth (d_t). This concept is apparent in that obvious changes take place in the characteristics of the thermal boundary region without corresponding changes in the physical depth of the hair. Changes in the shape of the temperature profile are related to air temperature, absorbed radiation, and wind velocities. The radiant temperature also changes.

A temperature profile shows the temperature in the hair-air interface at any given depth. The radiant temperature is an integration of the vertical and horizontal distribution of the temperature field exposed to the environment. This integration results in an average radiant temperature, which can be compared with the temperatures on the profile. The distance between the point on the profile at which the radiant temperature equals the profile temperature and the base of the hair can be determined, and this distance can be considered the thermal depth.

The effective thermal depth of the hair on the trunk of a deer is shown in Figure 13-15. As wind velocities increase, there is a reduction in d_t, equaling nearly 50% of the physical depth when the wind velocity is 14 mi hr^{-1}. A similar pattern is observed for sharp-tailed grouse, although the thermal depth is relatively less

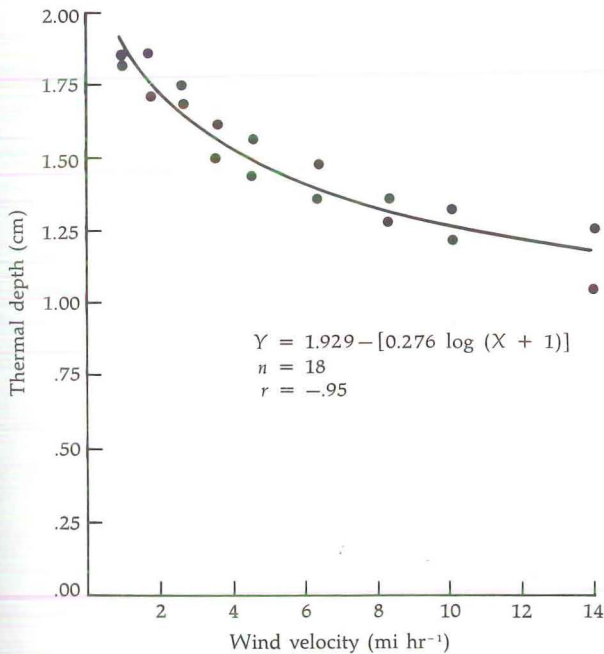$$Y = 1.929 - [0.276 \log (X + 1)]$$
$$n = 18$$
$$r = -.95$$

FIGURE 13-15. Effective thermal depth of deer hair on the simulator when exposed to different wind velocities. (From Stevens 1972.)

than the physical depth throughout the entire range of wind velocities (Figure 13-16). Current experiments at the BioThermal Laboratory indicate that the relationship between d_t and wind velocities depends on several factors, including hair structure and wind turbulence; the data in Figures 13-15 and 13-16 are applicable only to the flow characteristics during those tests.

13-6 GEOMETRY AND SURFACE AREA

Surface area is one of the most obvious parameters necessary for the calculation of the heat loss from an animal. The measurement of this parameter is exceedingly difficult, however, because of the complex geometry of an animal's body and its hair or feather surface. Physiologists have used many different methods, including skinning the animal and measuring the flat hide, using rollers across the animal's surface, and direct measurement with a tape.

Direct measurements with a fiberglass tape have been completed on 309 white-tailed deer ranging in age from a few days to several years (Moen, unpublished data). Twenty-two linear and circumferential measurements of each animal have been made (Figure 13-17), and the areas have been calculated using equations for cylinders, frustums of cones, and rectangles (see Appendix 5). The regression equations expressing the total surface area in relation to body weight for male and female deer are shown in Figure 13-18, with data points plotted

FIGURE 13-16.   Effect of wind speed on thermal depth of breast
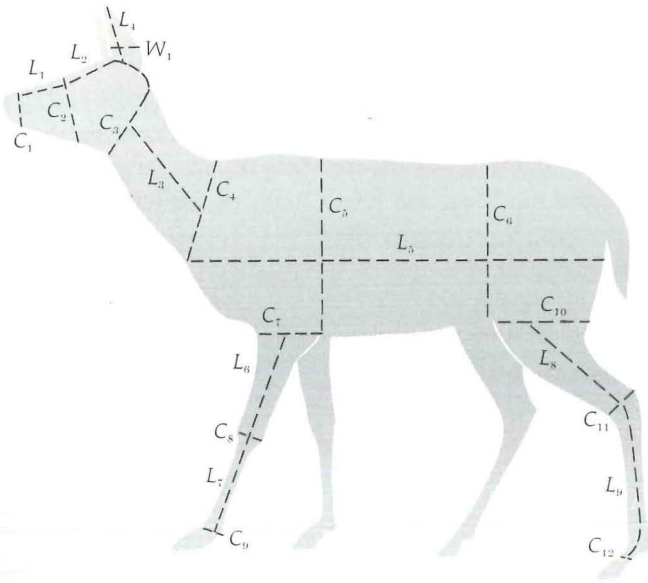and back feather tracts of sharp-tailed grouse. (From Evans 1971.)
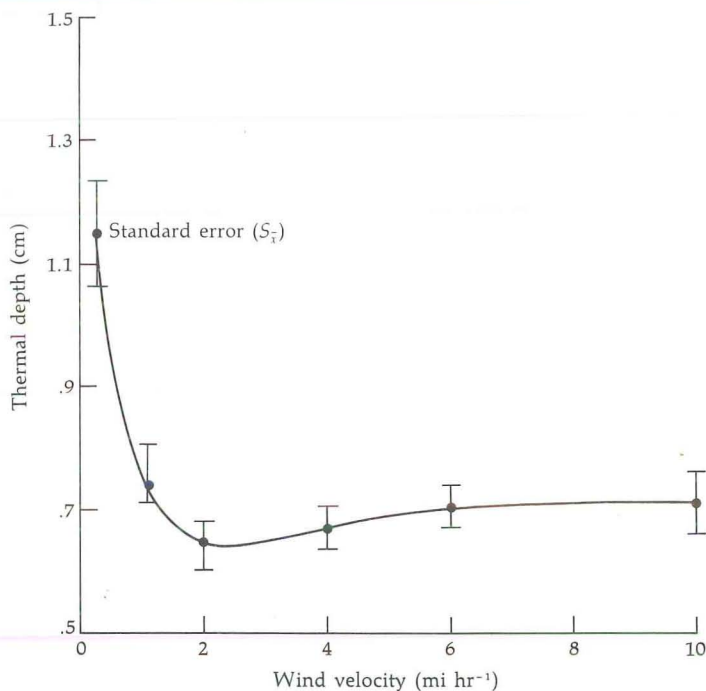
FIGURE 13-17.   Twenty-two measurements (C = circumference, L = length, W = width) have been used to calculate the surface area of white-tailed deer. The subscripts are identified in Appendix 5.

FIGURE 13-18.   The relationship between surface area and body weight of white-tailed deer. The data points are for females only.

Females: $Y = e^{-1.95 + 0.635 \ln x}$
$n = 135$
$r = .99$

Males: $Y = e^{-1.95 + 0.626 \ln x}$
$n = 146$
$r = .99$
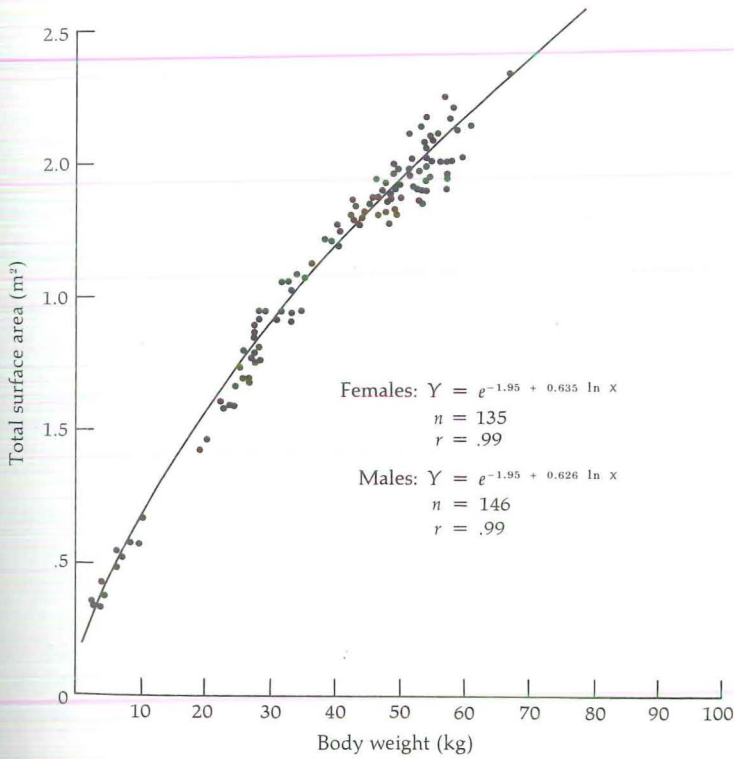
for females only. Variations between individual deer are fairly small; the correlation coefficients are high. Measurements taken by different people have also been found to be quite consistent. Equations for the head, neck, ears, trunk, upper front leg, lower front leg, upper hind leg, and lower hind leg for female white-tailed deer are listed in Appendix 5.

Measurements of the geometric components of sharp-tailed grouse have been made by Evans (1971). The equation is

$$\text{Surface area (cm}^2) = 7.46 \ W^{0.652}$$

Similar measurements have been made for pheasants up to 16 weeks of age at the BioThermal Laboratory (Figure 13-19). Regression equations for the surface area of the beak, head, neck, body, upper leg, metatarsus, and toes of pheasants are found in Appendix 5.

The several geometric portions of an animal's physical surface participate differently in heat exchange. The thin legs exchange heat at different rates than the trunk, for example. This suggests that it is necessary to consider a thermal profile that is based on the thermal characteristics of different body parts in

FIGURE 13-19.   Total surface area of ring-necked and Japanese green pheasants in relation to weight. Replicates are indicated by circles.

$$Y = 167.54 + 1.06X$$
$$r = 0.977$$
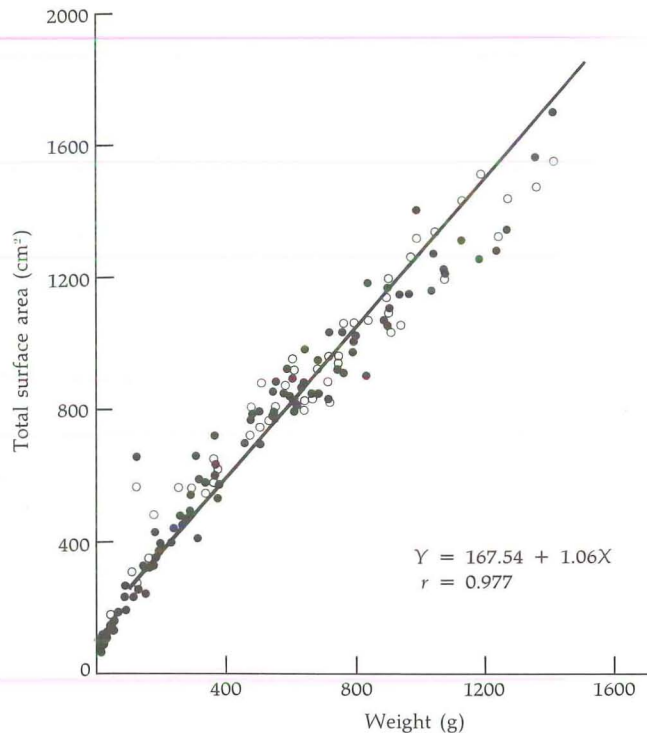
relation to their surface area, orientation, and other thermal characteristics and the distribution of thermal energy in the environment. This was discussed in Chapter 6 (see Figure 6-8) with reference to solar radiation.

13-7 THE CALCULATION OF HEAT LOSS

The complexity of heat exchange between animal and environment is beyond the capabilities of real-time analyses. The alternative is the use of a model in which some of the variables in the thermal equation are held constant. Posture is a variable, and two model postures—standing and bedding—can be compared. Wind velocities are continuously variable, and discrete velocities can be used in an analysis of wind effects.

The hair-air interface is the thermal barrier through which heat is conducted from the heat source to the heat sink. The metabolic heat lost from the surface of an animal passes through the hair-air interface at a rate that is dependent on the conduction characteristics of the hair layer. When the conduction characteristics are known and the radiation characteristics have been identified for particular weather conditions, the heat lost by convection can be determined as a residual. This basic concept is expressed in equation (13-1).

$$Q_k = Q_r + Q_c + Q_v \tag{13-1}$$

where

Q_k = heat lost by conduction through the hair-air interface
Q_r = heat lost by radiation from the thermal surface of the animal
Q_c = heat lost by convection from the thermal surface of the animal
Q_v = heat lost by evaporation

Specific values used in equation (13-1) are dependent on the particular model being analyzed. Appropriate geometric data for the model selected are used for the calculation of convection. A deer in a standing posture is composed mostly of cylinders and frustums of cones. Convection coefficients for these geometries have been calculated using the measured dimensions of deer. The vertical distribution of air flow past a deer in a standing posture varies, with the lower portions of the animal's body exposed to lower mean air velocities than the upper parts. The wind profile can be calculated as illustrated in Chapter 6. Evaporative heat loss is not considered in this model because its quantity appears to be quite small from the surface of a deer in cold weather.

Heat loss by conduction through the hair-air interface of a 60-kg deer standing in an open field with uniform radiation is shown in Figure 13-20. The heat loss by nonevaporative means is much greater at −20°C than at +20°C. The increasing effect of wind at −20°C, indicated by the steeper slope of the line, illustrates the greater importance of wind when the air temperature is low.

Note the convex curvature of the lines. This is due to the reduced effect of wind as velocities increase. This was illustrated for cylinders in Chapter 6 (Figure 6-17). The complex geometry of both the hair and the entire animal precludes the measurement of local convection losses directly, but they can be determined

as a residual when the other factors in equation (13-1) are known. When the convection losses are known, the "convective diameter" of the deer can be calculated.

The convective diameter (Figure 13-21) is an expression of the effective thermal diameter of the deer in relation to the efficiency of the convective process. Note that there is a marked increase in the convective diameter as the wind velocity increases from 0 to 1.5 mi hr^{-1}. This velocity range includes a transition from free to forced convection; it also indicates a rapid decrease in the efficiency of convection inasmuch as the tiny hairs become quickly linked to convection processes but the larger body cylinders are not yet efficient convectors. This was illustrated in Chapter 6 (Figure 6-17); the larger diameters are less efficient convectors, especially at the low wind velocities. The smaller thermal diameter observed when the air temperature is $-20°C$ illustrates the effect of increased convective losses at low air temperatures. The deer behave thermally like a smaller cylinder in the colder air.

The curves shown for each air temperature in Figure 13-21 reflect the separate curves that might be projected for the hair and the body separately, as indicated by the dashed lines ($+20°C$ T_a). Although these considerations may seem a bit detailed, they deserve some thought because of the indication that hair and body structure may play a more important role in heat loss than conductivity comparisons alone would indicate. Tracy (1972) comes to the same conclusion with respect to body size and the effect of wind on the conduction of heat through the hair layer of a mammal.

Further documentation of the importance of the role of the hairs in relation to the body is provided by the experiments on the interaction between radiation and convection discussed earlier in this chapter. The simulated cold night sky
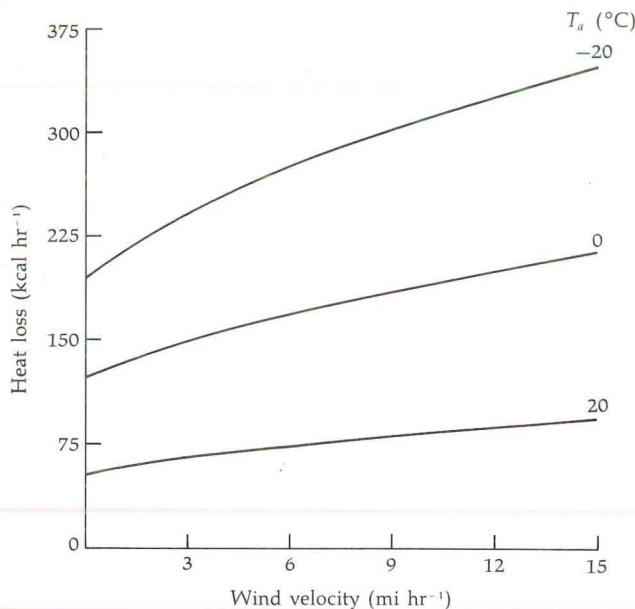

FIGURE 13-20. The calculated heat loss by conduction through the hair of a 60-kg deer. (From Stevens 1972.)
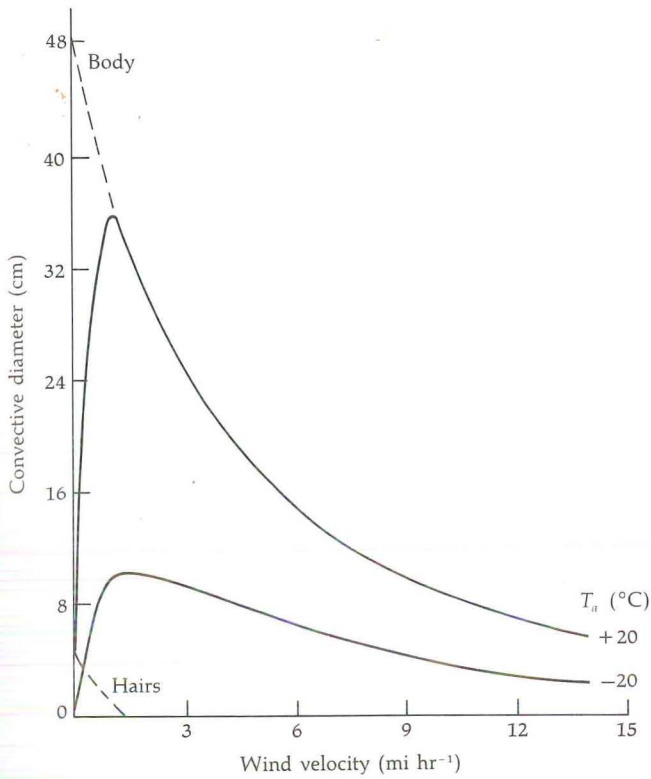
FIGURE 13-21. The whole body convective diameter of a
60-kg deer, expressing the relationship between gross body
diameter and hair diameter. (From Stevens 1972.)

was effective in reducing the radiant temperature of the hair surface only when
the wind velocity was less than 1 mi hr^{-1} (Moen, unpublished data). At velocities
greater than 1 mi hr^{-1}, the heat-sink effect was not observed, indicating that the
radiant temperature of the hairy surface was linked to air temperature rather
than radiant sky temperature. Since the clear sky at night is a heat sink, the effect
of wind flow across the hairy surface is "convection in reverse" inasmuch as heat
energy is added to the hair layer from the air in motion over the hairy surface.
This process is called advection.

The heat lost by conduction through the hair-air interface equals the sum of
the radiation and convection losses from the thermal surface of the animal (Figure
13-22). Convective losses increase at higher wind velocities. Radiation losses
decrease at higher wind velocities, because the cooling effect of wind reduces the
radiant temperature of the animal's thermal surface.

The relative importance of convection and radiation expressed in Figure 13-22
indicates that the effect of wind is much more important than the effect of radiant
energy in the cold, winter habitat. This suggests that the primary value of overhead
cover is its effect on wind velocities rather than its higher radiation flux. Early
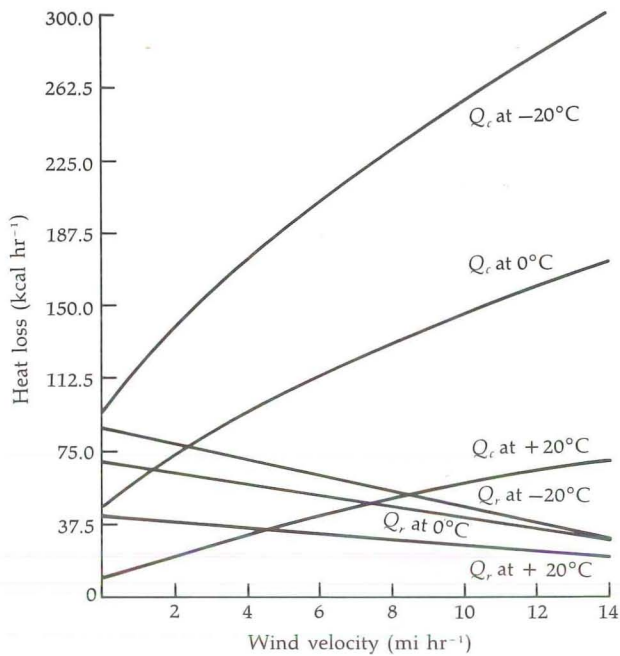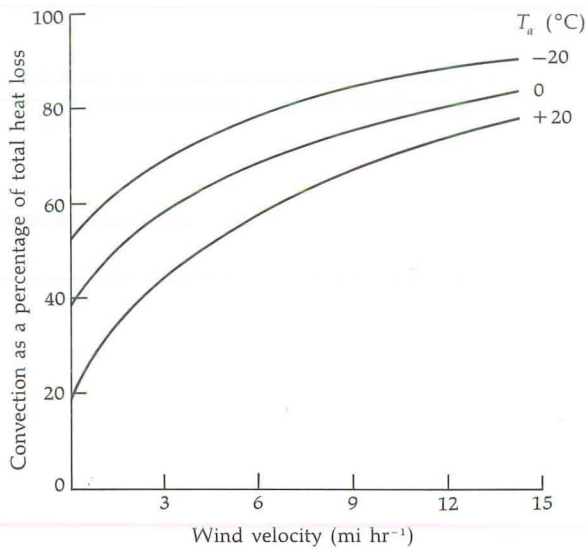
FIGURE 13-22.   Heat loss by radiation and convection from the thermal surface of a 60-kg white-tailed deer. Q_c = convection loss; Q_r = radiation loss. (From Stevens 1972.)

FIGURE 13-23.   Percentages of the total heat loss attributed to convection from a 60-kg deer in a standing posture at night. (From Stevens 1972.)

stages in succession—such as the shrub stage—may be very effective in reducing wind velocities and thus may be as good a thermal cover as a dense canopy.

The percentage of nonevaporative heat loss at three air temperatures that can be attributed to convection is shown in Figure 13-23. As wind velocities increase, convection losses increase in a nonlinear fashion, indicating a reduction in the efficiency of convection at the higher velocities. Convection is more important at low air temperatures, with free convection making up over 50% of the heat loss at $-20°C$, and rising to about 90% at that air temperature with a wind velocity of 14 mi hr^{-1}. These data are for a 60-kg deer; a smaller deer would have higher convective losses.

Calculating the percentage of the convective loss from different geometric components of the deer is interesting because theory suggests that the smaller cylinders, such as the lower parts of the legs, should be significant contributors to the convective heat loss. The actual percentages at different wind velocities are highest for the trunk (Table 13-2), but this is due to the larger surface area of the trunk and to the position of the trunk at a higher point in the vertical wind profile. The legs, with their smaller diameters, show a convective loss that is relatively greater than their surface-area percentages, thus conforming to theory on the effects of cylinder size.

One interesting characteristic of Table 13-2 is that the convection losses from the lower legs change less than the losses from the trunk at different wind velocities. This is due to the small cylinder size—the legs become linked quite quickly to low wind velocities—and to their position in the lower part of the wind velocity profile.

TABLE 13-2 PERCENTAGE OF HEAT LOSS BY CONVECTION AND RADIATION FROM DIFFERENT BODY PARTS OF A 60-KG DEER IN A STANDING POSTURE IN AN OPEN FIELD AT NIGHT WITH AN AIR TEMPERATURE OF $-20°C$

| Body Part	Percentage of Surface Area	*Percentage of Heat Loss at $-20°C$ and Different Wind Velocities (mi hr^{-1})*									
		Convection					*Radiation*				
		0	2	4	8	14	0	2	4	8	14
Head	6.6	4.6	4.8	4.8	4.7	4.5	8.2	8.9	9.8	11.9	17.1
Ears	2.4	9.4	7.9	7.2	6.4	5.8	3.1	3.4	3.7	4.6	6.5
Neck	7.6	3.2	4.2	4.7	5.1	5.3	7.5	7.2	7.0	6.4	5.2
Trunk	56.5	35.2	39.9	41.8	43.6	44.6	54.9	53.9	52.7	49.8	43.3
Upper front legs	5.0	7.4	6.6	6.2	5.8	5.5	5.7	6.1	6.5	7.5	10.0
Lower front legs	4.5	18.5	15.9	14.9	14.2	13.9	3.6	3.4	3.2	2.5	0.8
Upper hind legs	9.7	4.9	5.5	5.8	6.1	6.3	9.9	10.2	10.5	11.2	12.8
Lower hind legs	7.7	16.5	14.7	14.2	13.8	13.8	6.6	6.5	6.3	5.7	3.9

SOURCE: Data from Stevens 1972.

The percentages of the radiant heat loss from each geometric part show that the major portion of radiation loss is from the trunk. This is reasonable because of the trunk's sluggish response to convective forces and its large surface area. The trunk has a higher radiant surface temperature than the legs, and radiation loss is proportional to this radiant temperature.

The previous illustrations have included considerations of the radiant temperature profile of the animal, the thermal depth of the hair, the vertical wind profile, and the geometry of the animal in a standing posture. Convective losses have been treated as a residual, and the results are in agreement with basic theory. Knowledge of the convective loss permits the calculation of convection coefficients for the *whole* animal as illustrated in Figure 13-24, with weights from 20 to 100 kg and an air temperature of −20°C. The smallest deer loses less heat by convection than the largest one.

Expression of the convection coefficients on a unit-area basis indicates the effect of body size on the efficiency of heat loss (Figure 13-25). More heat is lost by convection from a square meter of surface of a small deer than from a square meter of surface of a large deer. The point of inflection is at a weight of 35 to 40 kg, indicating that animals over that weight become relatively less efficient as convectors and, conversely, more efficient in the conservation of heat energy. This weight range is similar to the average weight of fawns on many ranges in late autumn. These calculations lend substantiative evidence to the idea that fawns entering the winter period at below-average weights have certain physical laws operating against their chances of survival.

FIGURE 13-24.   Convection coefficients for the total surface area of white-tailed deer at an air temperature of −20°C. (From Stevens 1972.)
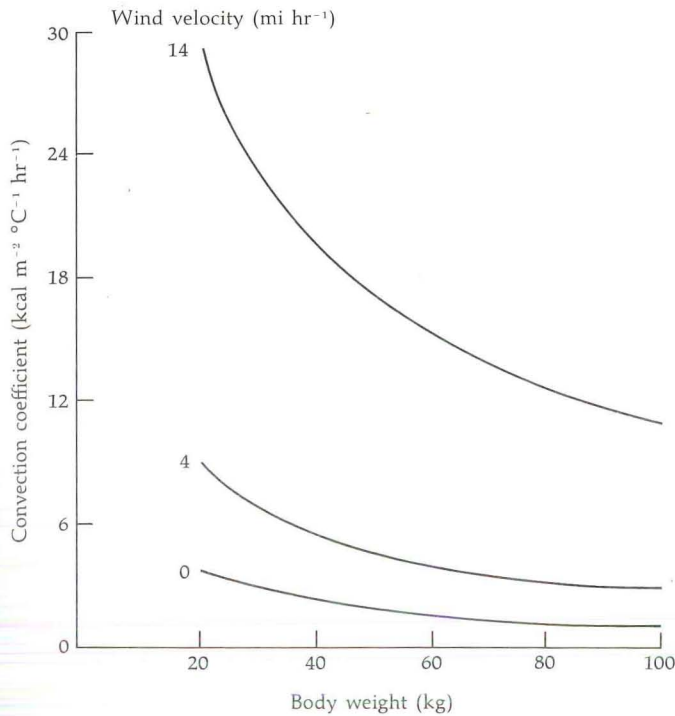
Wind velocity (mi hr⁻¹)
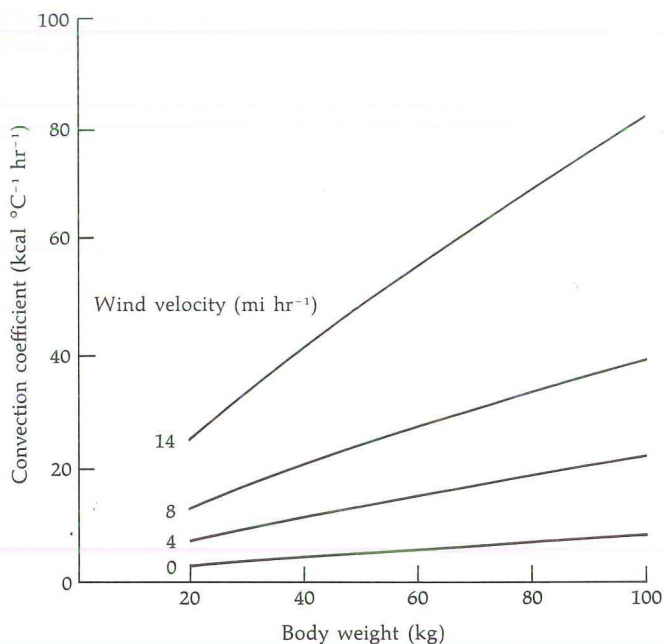
FIGURE 13-25. Convection coefficients calculated on a whole-body basis but expressed as kilocalories per square meter of surface area per hour. The air temperature is $-20°C$. (From Stevens 1972.)

LITERATURE CITED IN CHAPTER 13

Allen, T. E., J. W. Bennett, S. M. Donegan, and J. C. D. Hutchinson. 1964. Moisture in the coats of sweating cattle. *Proc. Australian Soc. Animal Prod.* **5:** 167–172.

Berry, I. L., and M. D. Shanklin. 1961. Environmental physiology and shelter engineering with special references to domestic animals; physical factors affecting thermal insulation of livestock hair coats. *Mo. Agr. Exp. Res. Bull.* **802:** 1-30.

Birkebak, R. C., R. C. Birkebak, and D. W. Warner. 1963. Total emittance of animal integuments. Paper #63-WA-20, presented at the Winter Annual Meeting, Philadelphia, Nov. 17–22, of the American Society of Mechanical Engineers.

Evans, K. E. 1971. Energetics of sharp-tailed grouse (*Pedioecetes phasianellus*) during winter in western South Dakota. Ph.D. dissertation, Cornell University, 169 pp.

Gates, D. M. 1963. The energy environment in which we live. *Am. Scientist* **51**(3): 327–348.

Hammel, H. T. 1953. A study of the role of fur in the physiology of heat regulation in mammals. Ph.D. dissertation, Cornell University, 105 pp.

Hammel, H. T. 1956. Infrared emissivities of some arctic fauna. *J. Mammal.* **37**(3): 375–378.

Moote, I. 1955. Insulation of hair. *Textile Res. J.* **25:** 832–837.

Riemerschmid, G., and J. S. Elder. 1945. The absorptivity for solar radiation of colored hairy coats of cattle. *Onderstepoort J. Vet. Sci. Animal Ind.* **20**(2): 223–234.

Stevens, D. S. 1972. Thermal energy exchange and the maintenance of homeothermy in white-tailed deer. Ph.D. dissertation, Cornell University, 231 pp.

Stevens, D. S., and A. N. Moen. 1970. Functional aspects of wind as an ecological and thermal force. *Trans. North Am. Wildlife Nat. Resources Conf.* **35:** 106–114.

Tracy, C. R. 1972. Newton's law: its application for expressing heat losses from homeo-therms. *BioScience* **22**(11): 656–659.

Tregear, R. T. 1965. Hair density, wind speed, and heat loss in mammals. *J. Appl. Physiol.* **20**(4): 796–801.

SELECTED REFERENCES

Alderfer, R. G., and D. M. Gates. 1971. Energy exchange in plant canopies. *Ecology* **52**(5): 855–861.

Billings, W. D., and R. J. Morris. 1951. Reflection of visible and infrared radiation from leaves of different ecological groups. *Am. J. Bot.* **38:** 327–331.

Birkebak, R., and R. Birkebak. 1964. Solar radiation characteristics of tree leaves. *Ecology* **45:** 646–649.

Fuchs, M., and C. B. Tanner. 1966. Infrared thermometry of vegetation. *Agron. J.* **58:** 597–601.

Gates, D. M. 1962. *Energy exchange in the biosphere.* New York: Harper & Row, 151 pp.

Gates, D. M. 1965. Energy, plants, and ecology. *Ecology* **46:** 1–13.

Gates, D. M. 1971. The flow of energy in the biosphere. *Sci. Am.* **224**(3): 88–100 (Offprint No. 664).

Gates, D. M., and C. M. Benedict. 1963. Convection phenomena from plants in still air. *Am. J. Bot.* **50:** 563–573.

Gates, D. M., E. C. Tibbels, and F. Kreith. 1965. Radiation and convection for ponderosa pine. *Am. J. Bot.* **52:** 66–71.

Hadley, E. B., and L. C. Bliss. 1964. Energy relationships of alpine plants on Mt. Washington, New Hampshire. *Ecol. Monographs* **34**(4): 331–358.

Hart, J. S. 1956. Seasonal changes in insulation of the fur. *Can. J. Zool.* **34:** 53–57.

Herreid, C. F., II, and B. Kessel. 1967. Thermal conductance in birds and mammals. *Comp. Biochem. Physiol.* **21:** 405–414.

Hutchinson, J. C. D., and G. D. Brown. 1969. Penetrance of cattle coats by radiation. *J. Appl. Physiol.* **26**(4): 454–464.

Idso, S. B., D. G. Baker, and D. M. Gates. 1966. The energy environment of plants. *Advan. Agron.* **18:** 171–218.

Joyce, J. P., and K. L. Blaxter. 1964. Effect of air movement, air temperature, and infrared radiation on the energy requirements of sheep. *Brit. J. Nutr.* **18**(1): 5–27.

Knoerr, K. R., and L. W. Gay. 1965. Tree leaf energy balance. *Ecology* **46:** 17–24.

Miller, P. C. 1971. Sampling to estimate mean leaf temperatures and transpiration rates in vegetation canopies. *Ecology* **52**(5): 885–889.

Morrison, P. R., and W. J. Tretz. 1957. Cooling and thermal conductivity in three small Alaskan mammals. *J. Mammal.* **38**(1): 78–86.

Raschke, K. 1960. Heat transfer between the plant and the environment. *Ann. Rev. Plant Physiol.* **11:** 111–126.

Tibbols, E. C., E. K. Carr, D. M. Gates, and F. Kreith. 1964. Radiation and convection in conifers. *Am. J. Bot.* **51:** 529–538.

Turrell, F. M., and S. W. Austin. 1965. Comparative nocturnal thermal budgets of large and small trees. *Ecology* **46:** 25–34.

Vogel, S. 1968. "Sun leaves" and "shade leaves": differences in convective heat dissipation. *Ecology* **49**(6): 1203–1204.