

14

PHYSIOLOGICAL, BEHAVIORAL, AND GENETIC RESPONSES TO THE THERMAL ENVIRONMENT

14-1 THE ROLE OF THE ANIMAL IN THERMAL ENERGY EXCHANGE

A homeothermic animal maintains a balance between its heat production and the physical processes of heat exchange with its environment by regulating its physiology and behavior. The complexity of heat transfer is beyond comprehension, but the characteristics of heat transfer for different animals in different habitats can be determined through analytical procedures. For example, evaporation losses are more important at high temperatures when vapor-pressure deficits are high, but little research has been done on evaporative loss from wild animals.

A series of thermal analyses, mostly for white-tailed deer, are presented in this chapter. It is difficult to illustrate dynamic heat exchange in two-dimensional graphs, but insight into the relative importance of different modes of heat exchange contributes to our understanding of the basic energy relationships between an animal and its environment.

The heat loss described in Chapter 13 must be balanced by an animal's heat production if homeothermy is to be maintained. An animal can either increase its heat production or reduce its heat loss to maintain homeothermy. These are regulated in several ways, both behaviorally and physiologically. The predicted energy balance, using a model, is discussed in this chapter, along with responses and adaptations described by others studying homeothermy and energy exchange. Before going on to specific responses, however, let us consider the concept of a "critical thermal environment" in relation to thermal energy exchange.

14-2 THE THERMAL REGIME AND THE CRITICAL THERMAL ENVIRONMENT

A homeothermic animal is in a continual state of dynamic equilibrium between heat production and heat loss. The continual adjustment of physiological and behavioral responses to the changing energy flux in the environment results in short-term temperature changes in the animal, but this is a normal part of life for a homeotherm. A *critical thermal environment* (Moen 1968) exists when the animal must make a response in order to maintain homeothermy. When the heat production of an animal is greater than the heat loss, even though the animal may attempt to maintain a balance, the animal is in a *critical hyperthermic environment*. If heat loss is greater than heat production, the animal is in a *critical hypothermic environment*.

Physiologists have defined a thermoneutral zone as the range of temperatures that do not cause a metabolic response to maintain homeothermy during basal metabolic measurements. This has been a useful definition for the establishment of a laboratory standard for comparative work, but it is quite inadequate for ecologists who are concerned with an animal in its natural habitat. This animal lives at an "ecological metabolic rate," and it may spend a considerable amount of time outside the physiologically defined thermoneutral range, yet it survives and reproduces.

Situations can develop in which the many factors that make up the thermal regime, including both heat-production and heat-loss factors, may result in a critical thermal environment that is partly independent of existing weather conditions. A deer being chased by dogs on a cool autumn day, for example, may be in a critical hyperthermal environment because running has caused a great increase in heat production. The weather conditions are not critical; running is the critical factor. A deer may be in a critical hypothermal environment during a spring rain when its winter coat is being shed and its thin new summer coat becomes soaked with water. The effect of this rain might be critical during this molt period, but would have been quite unimportant when the animal was still in winter coat. Thus the critical factor is the stage of the molt in combination with the rain.

Any factor that is a part of the thermal regime could become critical if other thermal conditions were near critical. In a high wind, for example, there could be a critical orientation of an animal that would result in a balance between heat production and heat loss. A critical wind velocity, critical radiation level, critical activity level, critical posture, or any other critical variable is meaningful only when all other thermal factors are identified.

Because there are so many different combinations of thermal factors for free-ranging animals, the traditional idea of upper and lower critical temperatures to identify the limits of the thermoneutral zone is entirely inadequate in field ecology. It has served a useful purpose in the laboratory where chamber conditions are quite well represented by a temperature measurement, but data from these simplified laboratory experiments cannot be applied to the dynamic thermal regimes of free-ranging animals. The disparate descriptions given in the literature of the effects of weather on different species of wild ruminants suggests that it is necessary to analyze basic thermal relationships between an animal and its

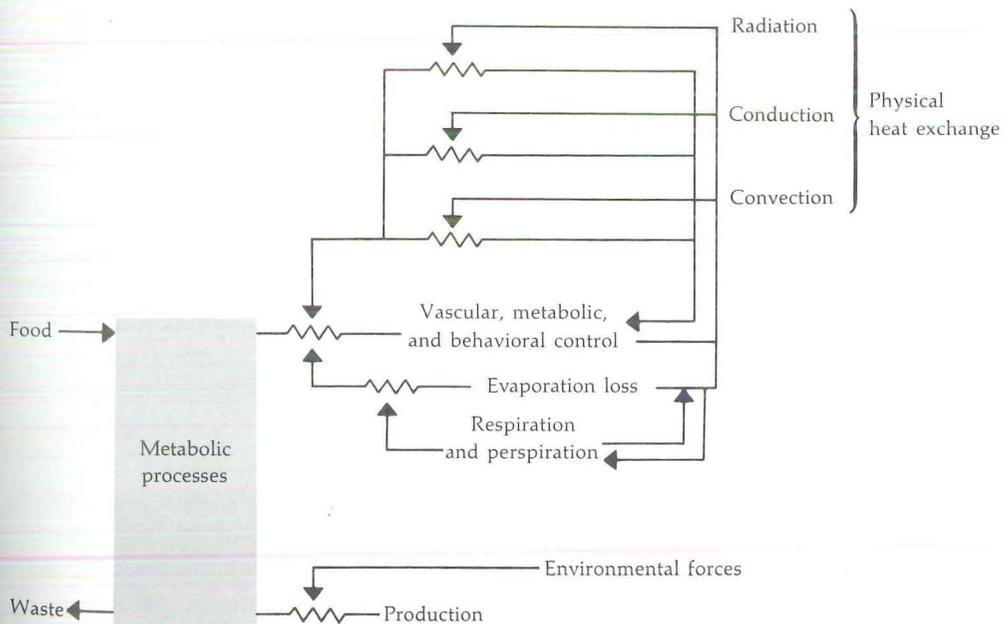
environment so that the physiological and behavioral responses to the thermal environment can be separated from the responses to social interaction between animals or to other stimuli that are not related in any way to weather factors. Thus the ecological definition of the thermoneutral range is a concept that requires an understanding of the principles of heat exchange instead of a precise set of factors with definite limits.

14-3 HEAT LOSS IN RELATION TO HEAT PRODUCTION

The control mechanisms available to an animal for maintaining a balance between heat loss and heat production can be represented conceptually with input and output energy. Food contains energy, and solar and infrared radiation also add to the heat load. Output energy includes the energy that goes into growth and reproduction, as well as the waste energy that has never been a useful part of the system (Figure 14-1). Note that there are several variables in this system, including vascular control over physical heat exchange, respiratory and perspiratory control over evaporation losses, behavioral control over physical heat exchange, and rate of heat production. The rate of production depends on the impact of such environmental forces as disease, social factors, and others on the physiological efficiency of the animal.

Predicted heat losses per hour for deer exposed to different wind velocities at an air temperature of -20°C are shown in Figure 14-2. The smaller deer lose less heat on an absolute basis, but the greater efficiency of heat conservation by

FIGURE 14-1. Regulatory and control mechanisms for the maintenance of a balance between heat production and heat loss.



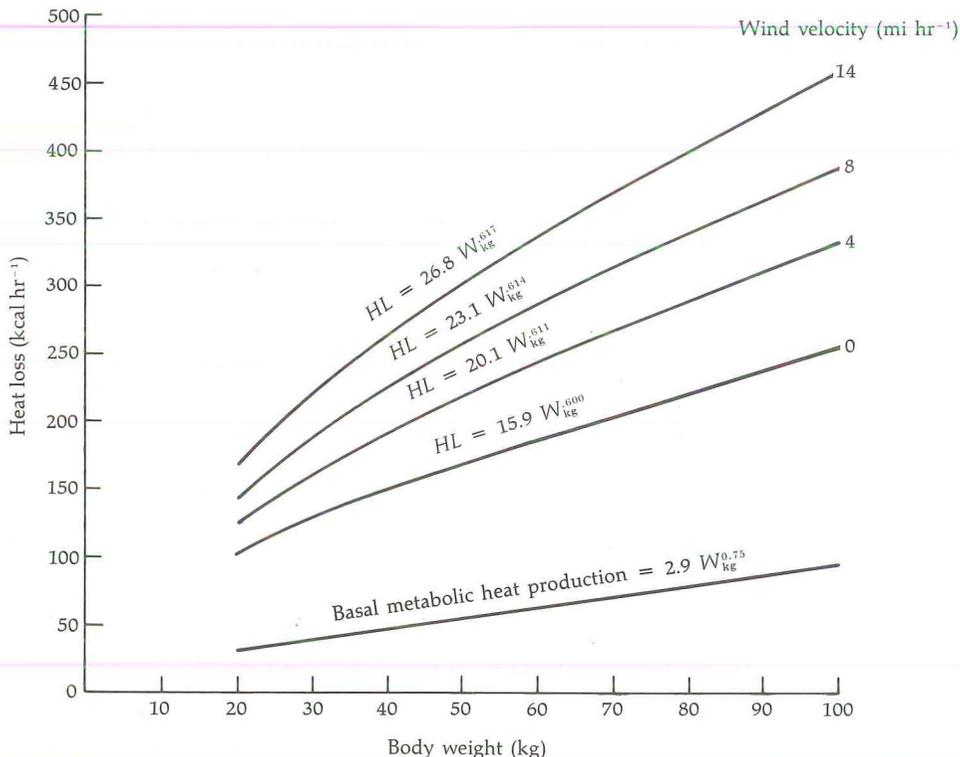
larger deer is indicated by the fractional exponent. Note that the exponents, ranging from 0.600 to 0.617, are less than the exponent used to express the relationship between heat production and weight (0.75). This indicates that a deer's efficiency in conserving heat is greater than its efficiency in producing it.

This illustration of heat loss is based on a standing model in an open field at night, which has been used because it represents the coldest habitat for a deer in the winter. Thermoregulatory mechanisms, such as vascular control in the extremities, metabolic responses, behavioral thermoregulation, feeding, activity, and others, can be used by deer and other species to regulate heat production in relation to heat loss. The complexity of these dynamic, constantly changing physiological and behavioral responses is beyond mathematical representation, but the use of models for specified sets of conditions provides an insight into the relative values of different responses.

14.4 PHYSIOLOGICAL RESPONSES TO THE THERMAL ENVIRONMENT

An animal's physiological responses to the thermal environment can be either (1) heat-producing or thermogenic or (2) heat-conserving. Three categories of an animal's metabolic responses to variations in the thermal environment over a

FIGURE 14-2. Total heat loss (HL) per hour from white-tailed deer expressed as a multiple of basal metabolic rate ($2.9 W_{kg}^{0.75}$). Air temperature is -20°C .



period of several days to several generations have been suggested by Folk (1966, citing Eagan):

1. "Genetic" adaptation: Used for alterations which favor survival of a species or of a strain in a particular environment, which alterations have become part of the genetic heritage of the particular species or strain. This is the same as acclimatization of the race.
2. Acclimatization: The functional compensation over a period of days to weeks in response to a complex of environmental factors, as in seasonal or climatic changes.
3. Acclimation: The functional compensation over a period of days to weeks in response to a single environmental factor only, as in controlled experiments.

These categories cover the range of possibilities over large increments of time, but what about the responses to short-term fluctuations that affect an animal's choice of bedding site, posture, or orientation with respect to the vegetative cover, the position of the sun, or wind characteristics? An animal is constantly employing heat-producing responses and heat-conserving responses in order to regulate body temperatures within certain limits.

Heat production is an active response involving the metabolism of absorbed nutrients or of body tissue. Heat conservation is accomplished by regulating an aspect of the animal-to-environment gradient, resulting in alterations in the dissipation of heat energy. In reality, these two processes occur together so it is the *net effect*—whether the heat production is greater or less than the heat loss—that is important in homeothermy.

THERMOGENIC RESPONSES. An animal may increase its heat production by increasing gross body activity or by increasing the rate of metabolism in specified organs or tissues. Raising the level of gross body activity is not 100% efficient since greater body movement results in greater heat dissipation due to the effect of movement in the hair-air interface. Heat exchange by convection is also increased as the animal moves through the air, increasing the effective wind velocity at its surface. More body activity results in an increase in the energy requirement also.

An elevated metabolic rate cannot be sustained without development of an oxygen debt and muscle fatigue, so sustained body activity is not possible during extended periods of cold weather. The daily metabolic rate of a free-ranging animal may result in an energy expenditure that exceeds the net energy in the food ingested because the animal has reduced food intake during the rutting season, because of a depleted food supply on the range, or for other reasons. In any case, energy stored in the body must be utilized, and a weight loss will ensue. Thus, an increase in body activity to maintain homeothermy is not a feasible short-term solution because of metabolic limits nor is it a feasible long-term solution because of limits imposed on the amount of weight loss that can be tolerated physiologically.

Less obvious but very important thermogenic responses are found in metabolic potentials that do not involve overt muscular activity. Animals conditioned to cold weather [acclimatization (Folk 1966)] are more capable of withstanding cold than animals that have had no previous exposure to cold. Rabbits and rats that were conditioned to cold temperatures did not become hypothermic or suffer frostbite, but unconditioned animals did when both groups were exposed to -50°C for 8 hours. Four yearling sheep that were exposed to temperatures as low as -20°F in a chamber had higher heart rates and lower rectal temperatures than four that were maintained in 55° – 65°F temperatures (Hess 1963).

A general relationship has been observed between heart rate, oxygen consumption, and heat production; the increased heart rate is indicative of a higher heat production. Heart rate in relation to oxygen consumption in sheep was studied by Webster (1967) who found a close relationship between heart rate and energy expenditure when the energy expenditure was increased by cold stress or increased levels of food intake. This general relationship between heart rate and metabolism shows considerable variation among individual animals, however, so it is necessary to calibrate each animal to determine the curve relating its heart rate to oxygen consumption.

The relationship between heart rate and oxygen consumption does not seem to hold true under hot conditions. Suggs (1965) did not find an increase in oxygen consumption in human subjects exposed to additional radiation, but this may be due to the necessity to dissipate heat, so increases in cardiac output were effective in elevating the amount of vascularization.

One metabolic response that has received considerable attention by physiologists is nonshivering thermogenesis (NST), which involves an increase in heat production that results from the metabolism of brown fat. Metabolic rates up to six times the basal rate have been reported for rats. Cold-adaptive nonshivering thermogenesis is not common to all mammals, however. Some species have a high capability for NST when young but much less when adult, and in larger species such as cattle it seems to be lacking altogether (Brück, Wünnenber, and Zeisberger 1969). They formulated a general rule, documented also by Jansky et al. (1969), that the bigger the animal, the less brown fat it possesses. This conclusion was reached after careful consideration of their own work and that of others reported in the literature. It appears that wild ruminants do not rely on NST for the maintenance of homeothermy.

The metabolic rate of white-tailed deer confined to a cold respiration chamber rises as the chamber temperature is lowered (Figure 14-3). The increase for four deer in winter coat is less than the increase for two deer in summer coat in May and June. The rate of heat production in May and June is greater than in the winter. The proportional increase in heat production as the chamber temperature is lowered from $+20^{\circ}\text{C}$ to -20°C is 1.7 times in the winter and 2.6 times in the summer coat. Thus the rise in heat production for deer in summer coat appears to be a function of the decreased insulation value of the summer coat and of changes in the metabolic characteristics of the animal.

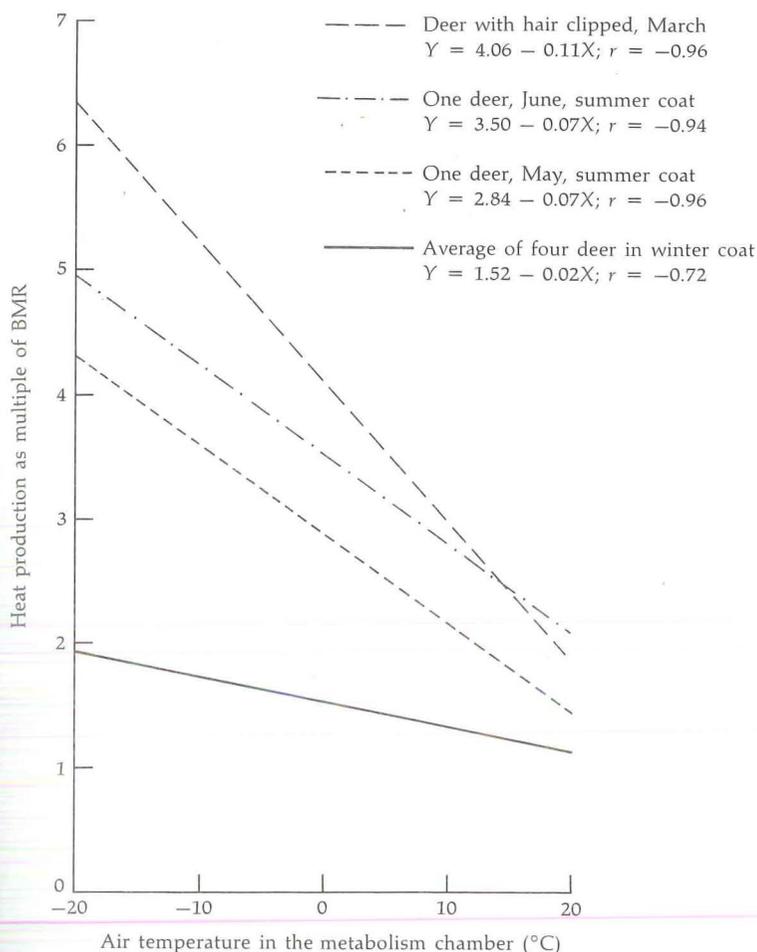


FIGURE 14-3. The relationships between heat production and air temperature in the metabolism chamber at the University of New Hampshire. (From Silver et al. 1971.)

The high metabolic potential of the deer ($6 \times \text{BMR}$) while confined to a chamber is shown in the results for the clipped deer. Since a metabolic rate of over six times BMR cannot be maintained because of physiological constraints, the measured rates of heat production in cold chambers cannot be applied directly to temperature data in the field. The experiments are useful, however, for determining the metabolic potential of the animal without a significant increase in gross body activity or for determining the effect of diet on heat production.

Another metabolic process that is important in thermogenesis in ruminants is the effect of the heat of rumen fermentation. The heat energy released during the exothermic fermentation process may contribute to the maintenance of homeothermy. The absorption and metabolism of nutrients that follows is an additional source of heat, attributed to nutrient metabolism. These heat increments are eliminated during basal metabolism measurements by imposing the standard condition of post-absorptive digestion.

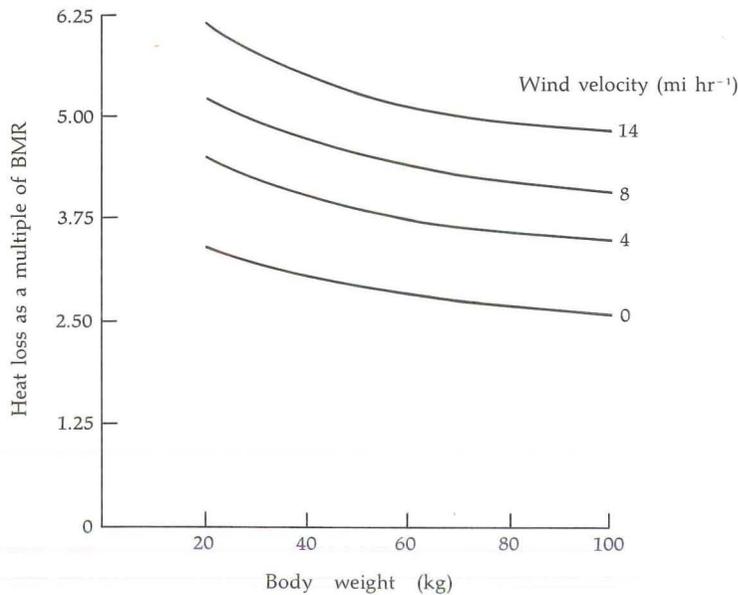


FIGURE 14-4. The predicted heat loss from a 60-kg deer in a standing posture at an air temperature of -20°C . (From Stevens 1972.)

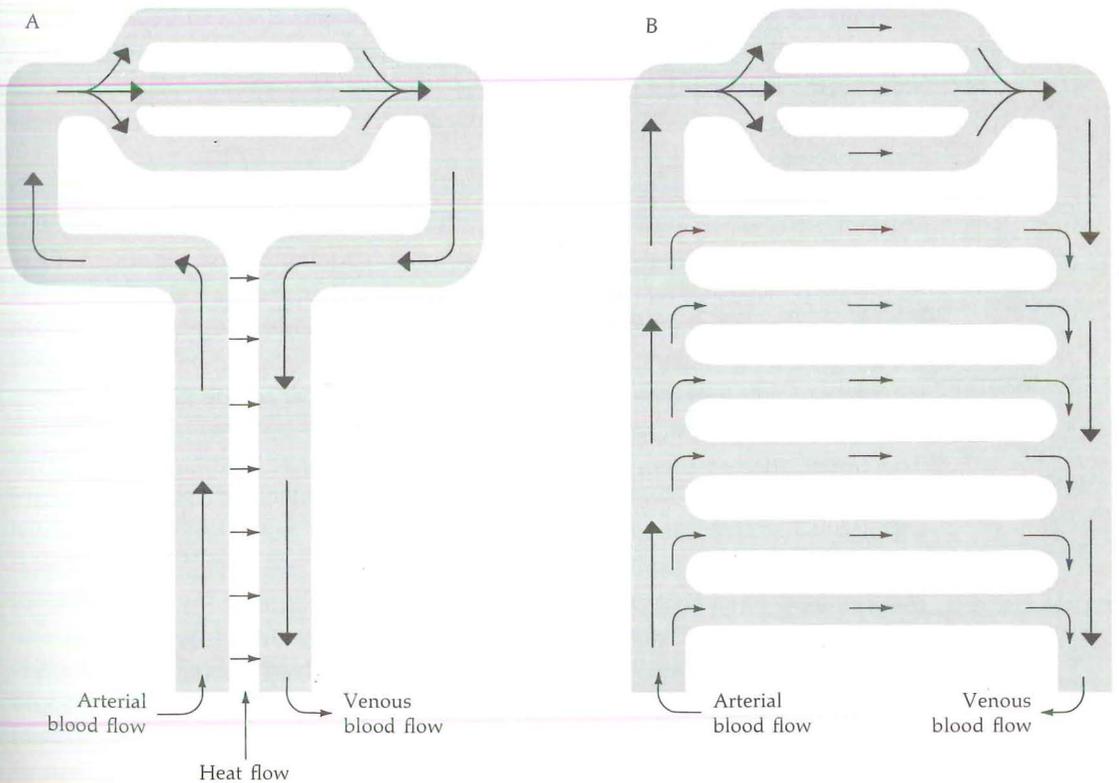
Experiments on sheep in chambers show that the critical temperature based on the chamber environment is higher when the sheep are at a low feeding level, lower at a medium feeding level, and lowest at the highest feeding level (Graham et al. 1958; Graham 1964). This pattern can be expected, but it must be emphasized that an animal has several alternative pathways to maintain heat production or regulate heat loss. In the absence of sufficient food, for example, fat catabolism occurs under cold conditions so that the heat production is maintained at a level necessary for the maintenance of homeothermy. New-born lambs, not yet developed as homeotherms, that were confined in a room at 23°C survived longer than those confined at 9°C , indicating that a lower heat production was possible because the warmer room resulted in a reduced rate of heat loss from the animal (Alexander 1962a). The rate of depletion of the fat reserve is an important consideration under these conditions; fat and carbohydrate reserves appeared to be exhausted when the animal was near death from starvation.

The predicted heat loss from a deer at an air temperature of -20°C is shown in Figure 14-4. The wind velocity of zero is most nearly like the conditions in the respiration chamber at the University of New Hampshire. The predicted results show the heat loss to be about three times the basal rate, although the measured results shown in Figure 14-3 are about two times the basal rate at -20°C . This discrepancy can be explained by the fact that the model used to predict heat loss did not include vascular responses. Thus any reduction in the blood flow to the legs or ears would reduce the heat loss below the predicted level. A discussion of simulations of these vascular controls follows.

THERMOREGULATORY RESPONSES. The homeothermic animal maintains a balance between heat production and heat loss by distributing the heat produced during normal life processes, increasing the heat production when the animal is in a critical hypothermal environment, and increasing the heat loss when in a critical hyperthermal environment. Heat production by metabolic processes takes place in specific areas of the body. Muscle metabolism and rumen fermentation, for example, are two localized exothermic processes. The heat energy released is distributed throughout the body by the circulatory system, which functions in thermal transport. This thermal transport is physically a passive process until the animal exhibits control over blood flow in order to maintain a thermal balance.

Another passive mechanism (Figure 14-5A) that has been suggested as one adaptation by which caribou maintain sharp temperature gradients in their extremities is a heat exchanger (Irving and Krog 1955). This arrangement permits the exchange of heat without an exchange of arterial and venous blood. The heat flow is simply a conduction process from the warm arterial walls through the body tissue to the cooler venous blood that is returning from the extremities. Hart (1964) has data for rabbit ears that indicate the possible importance of this mechanism for the conservation of heat. Five calories per milliliter of blood flow were lost to the environment, with 22 calories returned to the body via the heat

FIGURE 14-5. Mechanisms for the conservation of heat energy: (A) passive; (B) active.



exchanger. This results in a colder tissue temperature in the extremities, but it seems to be an adaptation that does not inhibit the normal functions of the tissue.

A vascular shunt is an active mechanism for the distribution of heat energy as the blood is shunted from an artery to a vein, diminishing the blood supply in the terminal capillary beds (Figure 14-5B). This results in a reduction in heat loss from the extremities since the blood flow is reduced, but it also causes a reduction in the oxygen supply.

Regulation of heat loss by the control of blood flow is not precise enough to result in a constant temperature at the extremities. Ear temperatures of caribou, for example, showed phasic changes from lows of nearly freezing (0°C) to 15°C , back to 0°C , and so forth (Irving, Peyton, and Monson 1956). This indicates that the different parts of a homeotherm's anatomy are not in thermal balance.

Henshaw, Underwood, and Casey (1972) have studied the peripheral thermoregulation in Arctic foxes (*Alopex lagopus*) and gray wolves (*Canis lupus*), two species that spend much of their lives in subzero ambient temperatures. These Arctic canines did not show phasic rewarming of their foot pads when immersed in a -35°C bath or standing on extremely cold snow. Without phasic circulation to prevent freezing, continuous temperature regulation is necessary, and these animals maintained a foot temperature just above the freezing point.

Vasoconstriction can serve to reduce heat loss by reducing blood flow to an extremity, thus reducing the loss of blood-borne heat. This physiological response has a lower limit of effectiveness, however, since hyperconstriction would result in tissue freezing. The predicted effects of vasoconstriction in the legs of deer are illustrated in Figure 14-6. As the air temperature becomes colder and the wind velocity increases, the importance of vasoconstriction increases. These data are for a standing deer; bedded deer with vasoconstriction could reduce the heat loss even further.

The importance of vascular control of heat flow is related to the insulation characteristics of an animal's coat, since heat energy dissipated from metabolic tissue must pass through this insulative layer. The amount of vascular control in the extremities is relatively more important because of the shorter, sparser hair there than on the rest of the body. The insulation quality of deer hair on the body trunk is illustrated by the steep temperature gradient between the skin temperature and the base of the hair; I found that at an air temperature of -20°C , the skin temperature of deer was 37°C , a gradient of 57° over a distance of 2 cm. The importance of blood flow and hair insulation is further modified by the distribution of subcutaneous fat. A fat layer reduces the heat loss from an animal's surface since fat tissue is a good insulator.

Piloerection of hair or fluffing of feathers has been considered a useful adaptation for conserving heat. The piliary system is "... a variable thermal resistance which accommodates a basic tissue heat production conditioned by animal size to a seasonal factor," according to Herrington (1951). The effectiveness of piloerection in reducing heat loss from deer has been analyzed by Stevens (1972). Changes in the physical depth (d_p) of 1.5 and 1.8 times the depth of the hair in normal lie cause a reduction in insulation of 15% in each case. The effectiveness of

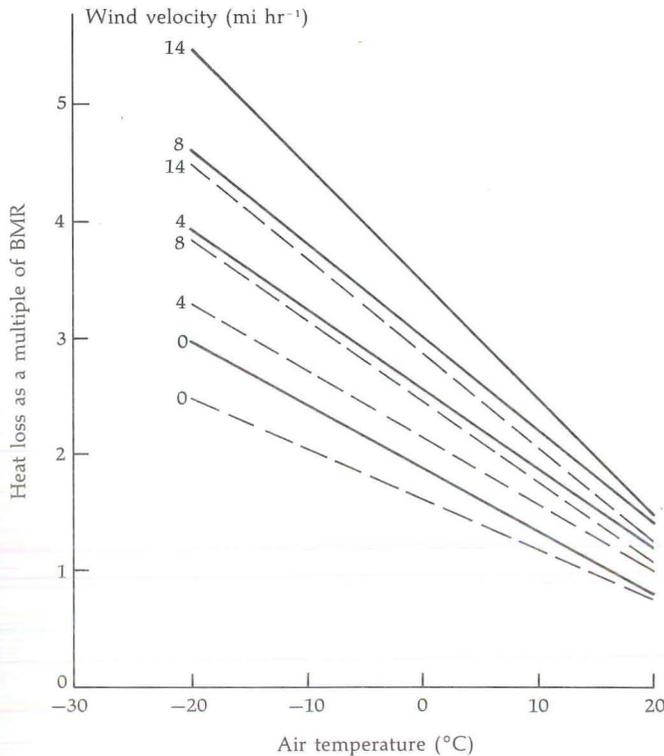


FIGURE 14-6. The effect of vasoconstriction on heat loss from a 60-kg deer: dashed line indicates vasoconstriction; solid line, no vasoconstriction.

piloerection as a heat conservation mechanism is greater at low air temperatures and high wind velocities (Figure 14-7).

Piloerection has traditionally been considered a heat-conservation mechanism because of the increase in the depth of the insulation layer. This increase is partially offset by the more open characteristic of the hair coat. The loss of heat through a more open hair layer is greater because of increased penetration by wind and subsequent convective heat loss. Thus the decrease in thermal conductivity due to the greater depth of erected hair is counteracted by the increase in heat flow through the more open erect hair.

An important function of piloerection in the maintenance of homeothermy that has not been investigated is its value as a heat-producing adaptation. This theory is illustrated in Figure 14-8. Under warm conditions, normal muscle tonus results in a small amount of heat production from chemical processes involved in muscular contraction. A small temperature gradient exists between the external surface of the skin and the subcutaneous muscle layer. As the environment gets colder, heat loss increases and the temperature gradient from skin to muscle increases in magnitude as the temperature decreases. Thermal receptors in the skin may then sense the colder conditions, the central nervous system relates the signal

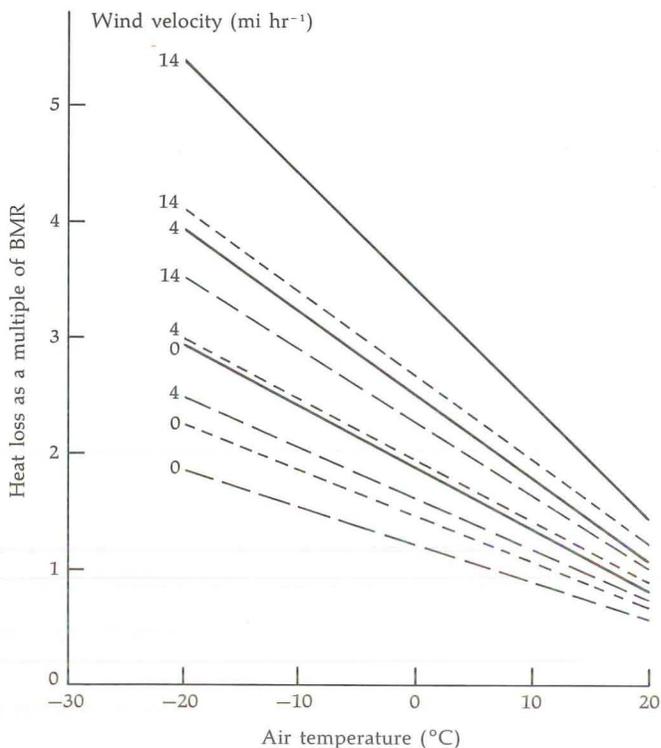


FIGURE 14-7. The effect of piloerection on heat loss from a 60-kg deer: solid line indicates normal piloerection; short-dashed line, 1.5; long-dashed line, 1.8.

to the muscle tissue beneath the skin, and the muscle tissue may contract with a concomitant release of heat energy. This heat energy reduces the temperature gradient and raises the temperature in that area of the skin. As the muscles contract and release heat, the hair is erected! Piloerection is then a secondary effect, and the exothermic muscular contraction is a heat-producing process of primary importance in altering the temperature gradients and subsequent flow of heat.

Evaporation of body fluids is a thermoregulatory response that often occurs under hot conditions. The balance between heat loss and heat production in hot environments can be regulated by a reduction in nutrient intake and an increase in evaporative losses. Under these conditions, a large amount of water is consumed during hot weather. When the effective environmental temperature is equal to or greater than body temperature, evaporative heat loss is the only kind of heat loss possible. Radiation, conduction, and convection contribute to an increase rather than a reduction in body temperature.

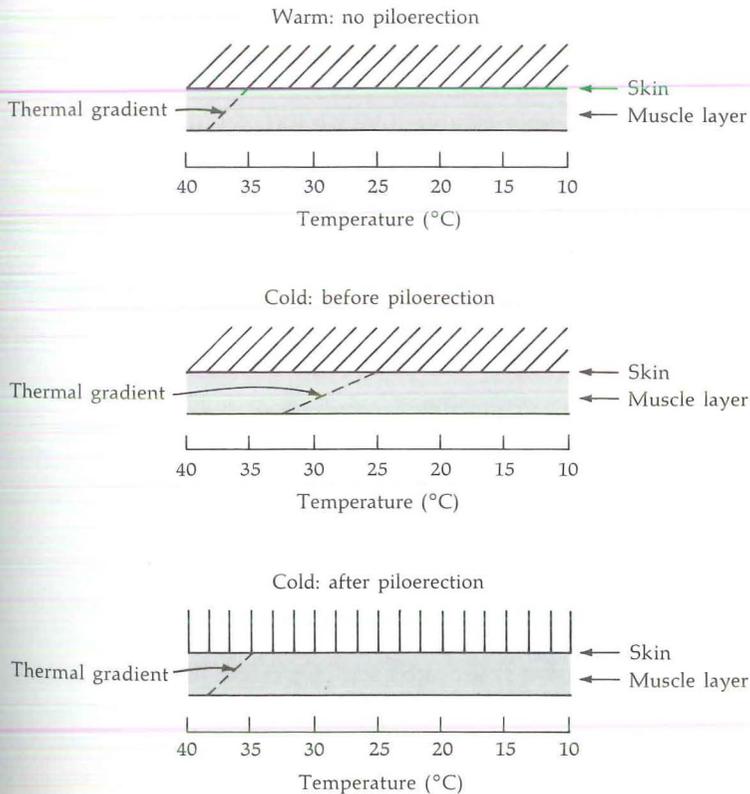
There are two sources of evaporation: the moist surface of the respiratory system and skin moistened by perspiration. The relative importance of each source depends on current thermal conditions and the species. Some animals such as cattle do not perspire very much, although horses perspire profusely.

In sheep with and without sweat glands, evaporative losses from respiration are more important than those from sweating, although sweating is advantageous to the shorn animal (Brook and Short 1960). Alexander and Williams (1962) conclude that newborn lambs do sweat, but respiratory water loss is more important in a hot environment.

The evaporative heat loss from respiratory surfaces can be increased by panting. This has often been considered an inefficient process because exothermic reactions take place as muscles are used for panting. This increases heat production, which must be offset by an increase in heat loss by evaporation. There are few data available that provide an indication of the relative magnitude of the two opposing forces. Hales and Findlay (1968) suggest that it may be more efficient than is generally supposed.

The loss of heat by evaporation is a desirable physiological response only when there is a sufficient supply of water. Two large African antelopes, the eland and the oryx, can survive with little or no free water. The oryx is capable of withstanding high internal temperatures by the presence of a countercurrent system involving respiratory cooling in the nasal passages that results in a brain temperature that is lower than the rest of the body. The eland has metabolic control that

FIGURE 14-8. A schematic representation of the heat-production function of piloerection.



parallels the thermal characteristics of the environment, seeking shade during the heat of the day to minimize a rise in body temperature (Taylor 1969).

There are times when the wetting of an animal's surface results in an undesirable increase in heat loss by evaporation, which may be counteracted by an increase in heat production. For example, wet lambs have a higher heat production than dry ones (Alexander 1962*b*). This relationship was also shown in Table 6-6 for infant caribou: Calves with wet fur had a heat production as high as ten times the basal rate. Such heat losses due to evaporation have been suspected to be a cause of mortality in the newborn of several species. Analytical studies of newly hatched game birds exposed to prolonged wet weather may reveal a considerable amount of information on mortality in the wild at this critical age.

Several other physiological responses are observed when animals are exposed to thermal regimes that are beyond the zone of thermoneutrality for any length of time. Body growth and production is retarded in hot environments, and reproduction is generally less successful. Critical hyperthermal environments for a few hours or days can result in mortality since the body tissue of most species is not adapted to the maintenance of metabolic processes at temperatures much over 2°C above normal.

The physiological effects of cold environments are frequently less critical than those of hot environments. The effect of cold environments can be compensated for by higher planes of nutrition that permit a level of heat production up to the maximum metabolic potential of the animal. It is extremely important to recognize that food is the ultimate source of energy for metabolic processes; radiant and atmospheric energy present during warm weather can only serve to reduce thermal gradients.

A response to a cold environment exhibited by white-tailed deer and possibly other animals considered to be homeothermic is a reduction in body temperature as an animal becomes lethargic in cold weather. This response has been observed in our current experiments using physiological telemetry equipment. It is a useful response for a free-ranging animal because it reduces its energy requirements on an already restricted winter range, which may be very important for survival and reproduction.

14-5 BEHAVIORAL RESPONSES

Animals respond behaviorally to the thermal regime, altering the balance between heat loss and heat production by changes in orientation, posture, activity, or the selection of cover. This behavioral thermoregulation has an effect on the physiological responses that result from thermoregulation, since behavioral responses cannot be made without the contraction of muscles. Thermoregulatory behavior—of both an individual and a group—includes thermogenic responses and heat-conservation responses, and it is the latter that are discussed in this section.

INDIVIDUAL RESPONSES. Each individual animal can assume a posture that will result in the conservation or dissipation of heat. For example, the surface area

of an animal that is in contact with the snow or soil is an important consideration in determining the amount of conductive heat loss. A standing animal has little area in contact with the substrate, so conduction losses are small. A deer bedded in the snow may have about 30% of its surface area in contact with the snow, and heat loss by conduction is an important part of the total heat loss. Figure 14-9 shows the amount of heat lost from a 60-kg deer in standing and bedded postures. The difference between standing and bedding is clear, with small differences due to the position of the head while bedded. The effectiveness of bedding posture as a heat conservation mechanism in the total thermal regime is relatively greater at higher wind velocities and colder temperatures. The predicted heat loss of a bedded deer is about two times basal at an air temperature of -20°C , so heat-production mechanisms, such as activity, may be employed to compensate. An alternative is for the deer to allow heat loss to exceed heat production, resulting in a drop in body temperature as the animal progresses toward a lethargic condition.

Many descriptions of thermoregulatory behavior are found in the literature. Severinghaus and Cheatum (1956) report that deer will remain in a bed for one to three days after a storm, usually under low-hanging conifers or windfalls. This observation may be related to the lethargic responses we have seen in our current experiments. In subzero weather in Maine, beds were found under conifer branches that were bent down and covered with snow, or under hardwoods that had retained their leaves (Hosley 1956). On very cold nights, deer in the Adirondacks were observed moving slowly on the trails, and Severinghaus and Cheatum

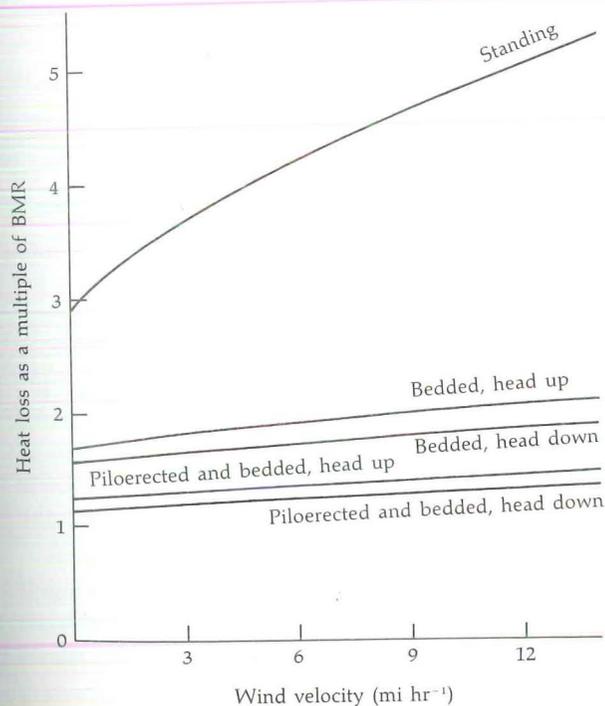


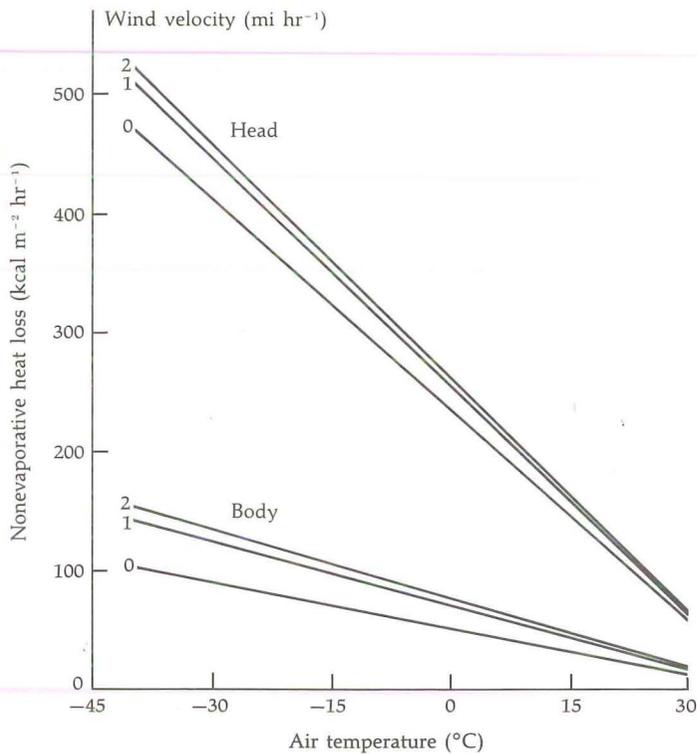
FIGURE 14-9. The effect of posture on heat loss from a 60-kg deer at an air temperature of -20°C .

(1956) suggested that it was too cold for the deer to remain bedded. They also cite several cases in which deer moved to seek shelter from cold winds.

Sharp-tailed grouse can exhibit thermoregulatory control by altering their posture. The heat loss from the head is much higher *per unit area* than that from the body (Figure 14-10), indicating that thermal benefits would accrue if the head and neck were withdrawn or curved back under a wing. Predicted thermal benefits from this postural change in different air temperatures and wind velocities are shown in Figure 14-11. Note that the least amount of head exposure is most beneficial at 0 mi hr⁻¹; 1.5 × BMR could be maintained with 5% head exposure down to about -8°C.

All calculations of the thermal balance between heat production and heat loss in different thermal regimes indicate that wind is the most important factor at low air temperatures. Calculations by Robbins (1971) indicate the importance of wind in altering the heat loss in different cover types (Figure 14-12). Wind velocities of 10-20 mi hr⁻¹ in an open field raise the predicted heat loss above realistic limits, whereas the effect of a conifer canopy in reducing wind velocities puts a 30-kg deer in a much more stable thermal balance. This effect and the effect that a conifer canopy has on snow depths and structure are benefits that must be considered in evaluating different cover types. It must be pointed out,

FIGURE 14-10. Effect of wind speed, air temperature, and body part on predicted heat loss through the feather layer.



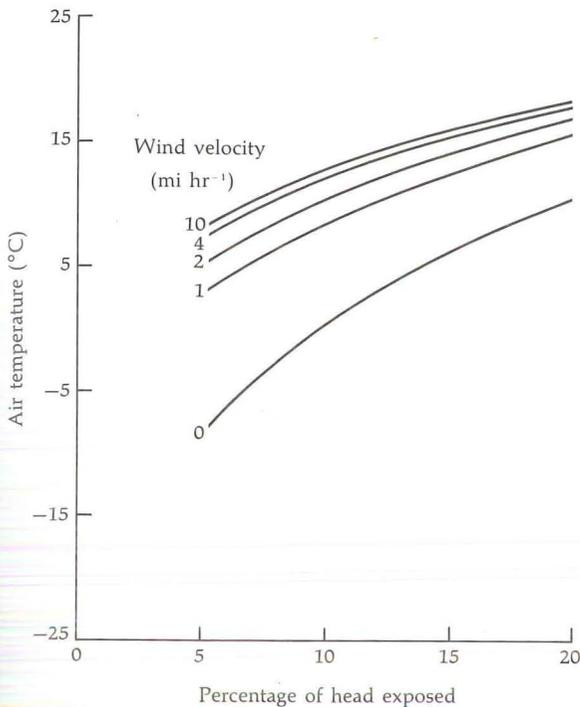


FIGURE 14-11. Effect of wind velocity and head exposure at ambient temperature at which predicted nonevaporative heat loss by a 1000-gram grouse would be $1.5 \times \text{BMR}$.

however, that a conifer canopy reduces food production so that a very essential source of energy is reduced. Further, topography and herbaceous and shrubby vegetation in more open habitats may reduce the wind effects nearly as much as a conifer canopy while producing a considerably greater quantity of food.

The relative benefit of herbaceous vegetation from 0 to 100 cm in height for deer of different weights is shown in Figure 14-13. The smallest deer benefits the most from the reduction in wind because it is in the lower part of the wind profile where the vegetation has its greatest effect on wind velocities. Small animals such as rabbits and hares, fox, game birds, and others can benefit from the use of low vegetation to reduce the wind velocity past their bodies; effective winter cover is not necessarily a dense coniferous overstory!

Henshaw (1968) noted that caribou bedded in areas of irregular topography during continued high winds. Their bodies were generally broadside to the wind. No apparent discomfort due to a low temperature with little or no wind could be detected. Observations of white-tailed deer in the cold, continental climate of western Minnesota also indicated that cold temperatures without wind had little or no apparent effect on their behavior. (Moen 1966).

An animal can exhibit many energy-conserving responses at one time, and no single order of their occurrence has been observed. Suppose that a 60-kg deer were standing in an open field at night, the coldest possible postural thermal model. At a wind velocity of 14 mi hr^{-1} , a negative thermal balance could be predicted, if the deer had a metabolic rate of two times basal, at 15°C (Figure

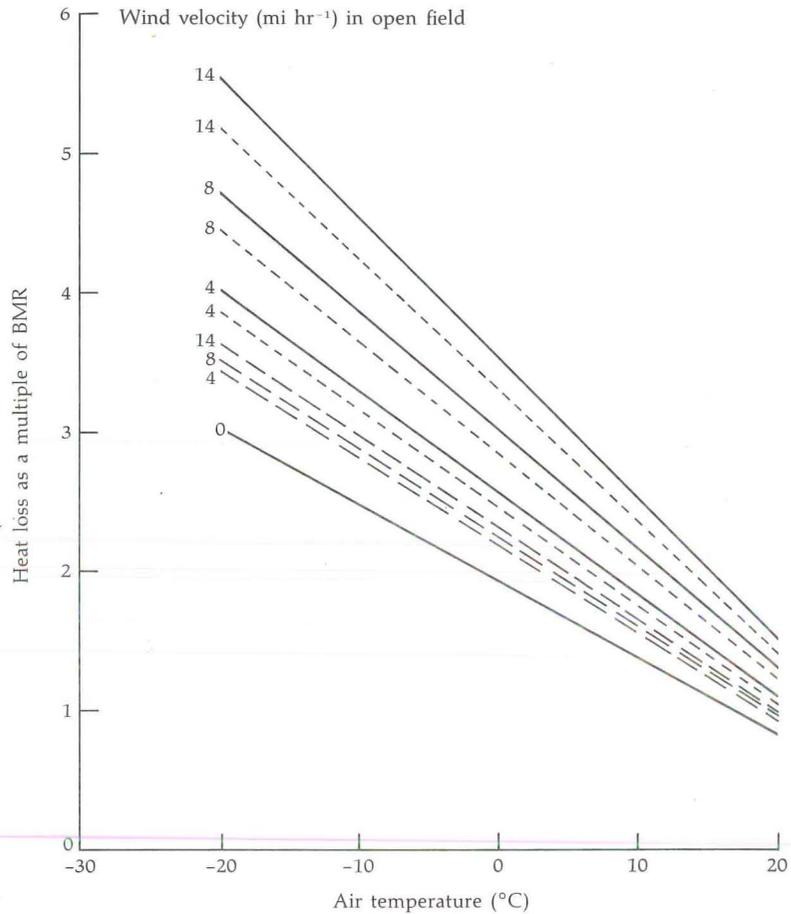


FIGURE 14-12. The effect of cover on heat loss from a 60-kg deer: solid line indicates open field; short-dashed line, hardwood; long-dashed line, conifer. (Data from Stevens 1972.)

14-14). A sequence of energy-conserving responses might be as follows: vasoconstriction, piloerection, both vasoconstriction and piloerection, bedding, the head could be placed down alongside the body, and finally at -40°C several mechanisms could be employed and the deer could still be losing heat at a rate less than $2 \times \text{BMR}$. This indicates that deer have a considerable potential for withstanding cold weather if they have a source of energy for heat production, and further capabilities if they can become lethargic during periods of cold weather.

One aspect of the heat-production-heat-loss relationship currently under investigation, using physiological telemetry techniques, is the reduction in heart rate, respiration rate, and body temperature when deer are exposed to cold

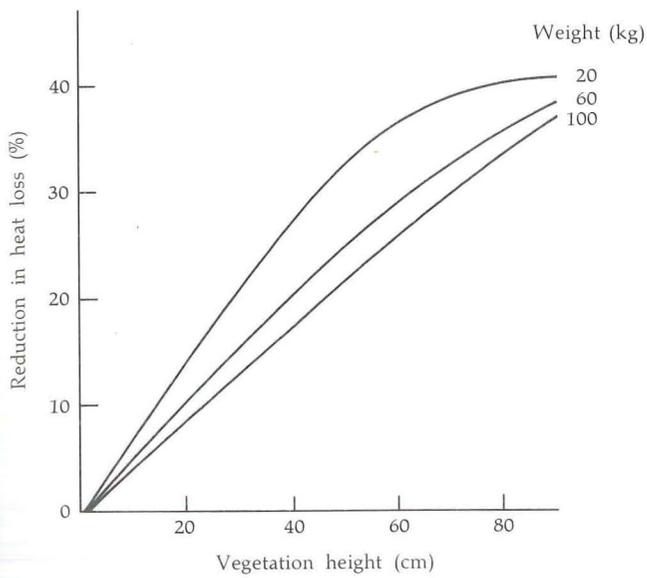
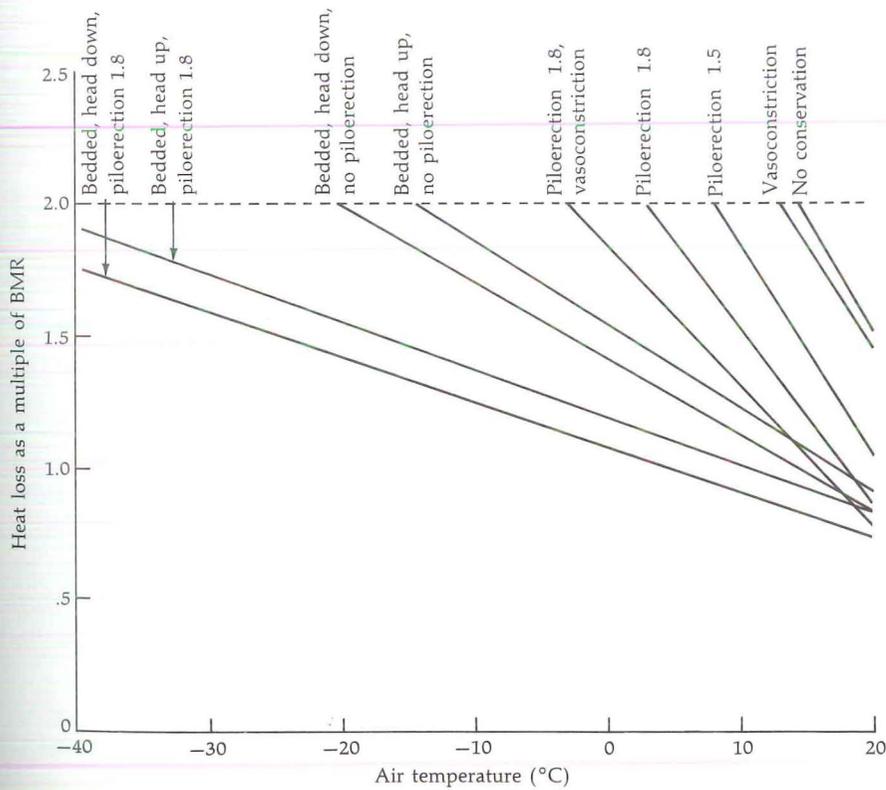


FIGURE 14-13. Reduction in total heat loss of a standing deer by vegetation, expressed as the percentage of decrease in heat loss from that of a deer in vegetation that is 0.75 cm in height with a 14 mi hr^{-1} wind at 2 meters.

FIGURE 14-14. Possible physiological and behavioral responses for maintaining heat loss below $2 \times \text{BMR}$ for a 60-kg deer in a 14 mi hr^{-1} wind.



weather. These reductions indicate that heat production must also be going down. Thus the dynamic response of the animal seems to be one of heat conservation rather than the more energetically costly heat-production response.¹

GROUP RESPONSES. Groups of wild ruminants seem to respond to general weather conditions in somewhat predictable ways. Caribou have been observed to be more gregarious during cold weather (Henshaw 1968). White-tailed deer move to or are confined to yards, especially during a winter with deep snow. In western Minnesota they form larger groups during periods of reduced visibility without apparent relation to cold weather (Moen 1966). Elk migration from the summer to winter range seems to be triggered by weather changes. Heavy snowstorms cause mule deer to migrate to a winter range in the fall whereas the migration back to the summer range is related to plant growth (Russell 1932). Moose bed in soft snow, which may reduce the energy requirements of the animals because snow is a good insulator (Des Meules 1964).

Studies have been done to evaluate the different directions of slopes that are used, and the usual conclusion is that southern exposures are used more than northern ones. There is a greater energy flux on south slopes than on north slopes because of the distribution of solar radiation. Northerly winds are also more common in the winter, resulting in generally harsher conditions on north slopes. The preference for south slopes may not be related only to current weather conditions. Snow depths are frequently less on south exposures, especially in late winter and early spring when melting begins. A decrease in snow cover results in an increase of available food, and this may have a considerable effect on the distribution of animals.

The grouping of animals has potential benefit in the reduction of heat loss. Animals that are huddled together exchange heat with each other, thus conserving it within the group. Caribou move in bands when feeding and the water vapor released by respiration sometimes condenses and forms a cloud that can reduce heat loss by radiation. However, this "cloud cover" may have little real benefit since the heat production of the animals is higher when they are active and the cloud is likely to be unnecessary for the maintenance of homeothermy. The physiological benefits from grouping may be social, with heat conservation benefits only incidental.

The distribution of energy in field habitats can be interpreted in a meaningful way only when the physiological benefits are related to environmental energy. Further, it is difficult to separate the physiological causes of behavioral responses from social causes. The physiological benefits from behavioral responses can be quantified more easily than the social benefits can because the basic unit of energy, the calorie, can be used. No such unit exists for the quantification of social traits, and interpretation is much more subjective.

¹These responses will be discussed in detail in a Ph.D. dissertation in preparation by Nadine L. Jacobsen, graduate assistant at the BioThermal Laboratory.

14-6 GENETIC RESPONSES

All animals exhibit individual variation owing to genetic differences. The obvious characteristics, such as coat color, body size, and so forth, are often the only characteristics considered by field biologists in studying particular populations. Since energy metabolism is vital to the survival of an individual animal, genetic factors that affect its energetic efficiency may have a significant bearing on its survival, especially when conditions of stress begin to appear.

Evans and Whitlock (1964) discuss the genetic adaptation of sheep to cold environments. A subtle but perhaps vitally important genetic characteristic that has been isolated in sheep is the inheritance pattern of the hemoglobin type. They point out that sheep breeds indigenous to cold environments tend to have high gene frequencies for hemoglobin A. This in turn is associated with a high efficiency of oxygen transport.

Hemoglobin is a blood protein with four iron-containing heme groups attached to it. Oxygen unites reversibly by combining with one of four iron atoms in the hemoglobin (HbO_2) molecule. Thus a fully saturated hemoglobin molecule contains four oxygen atoms, and is called oxyhemoglobin. Since oxygen is required for energy metabolism the efficiency of an animal's oxygen transport system may have a direct influence on its survival when exposed to cold conditions. Further, sheep with a low erythrocyte volume and related oxygen transport efficiency have a smaller chance of surviving a natural challenge by the parasite *Haemonchus contortus*, a helminth parasite of ruminants usually found in the abomasum, than does an animal with a greater metabolic efficiency. This parasite has been found in deer. The combined effects of cold weather and a parasite load may require a highly efficient metabolic system if a deer is to survive.

Owing to the effects of natural selection, different deer populations may have genetic adaptations—such as hemoglobin types—that result in higher survival rates. One complicating factor, however, in the process of natural selection is the effect of man on the distribution of wild ruminants. The Adirondacks of New York and the coniferous forests in northern Minnesota, for example, were not inhabited by deer populations prior to the settlement of North America by the white man. Woodland caribou and moose were present, but the opening of the forests by timber-cutting operations caused a decline in the number of caribou and moose and an increase in the number of white-tailed deer. Thus the white-tails are now found in areas that have weather, soil, and forage characteristics that may be quite different from those in presettlement deer ranges. The normal patterns of genetic evolution have been further complicated by the transplanting of deer from one geographical region to another. The period of time since settlement and the transplanting of deer is but a fleeting moment on the evolutionary scale, and the genetic characteristics of present populations may not result in maximum metabolic efficiency.

There are daily and seasonal metabolic cycles that are inherent in different species. Generally, the metabolic rate is higher during the day for diurnally active animals, and higher at night for those that are nocturnal. Many animals have

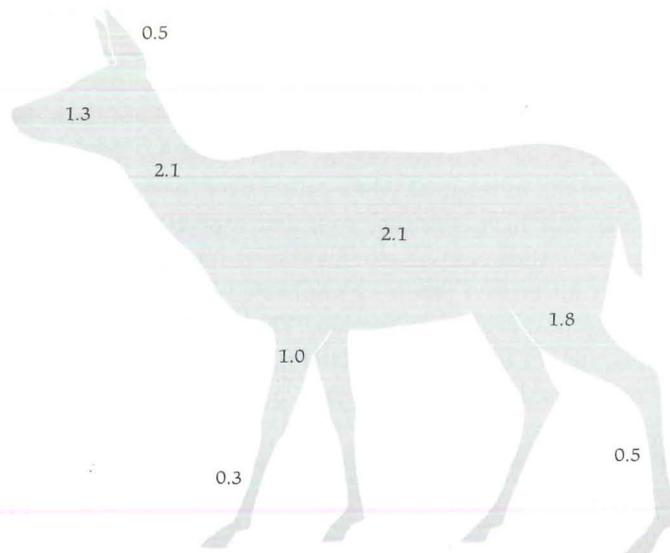
seasonal metabolic rhythms—hibernation is an extreme example. Deer appear to exhibit a seasonal rhythm with lower metabolism in the winter (Helenette Silver, personal communication; Moen and Jacobsen, unpublished data).

Basal metabolic rates are similar for tropical and arctic animals, but the thermal characteristics of the hair coat are vastly different. It is generally recognized that the insulation of the coat is the major adaptation of northern species. There are marked differences in the depth and structure of summer and winter coats of white-tailed deer. Their summer coats of finer hair are not nearly as thick as their winter coats. The depth of winter hair at several points on whitetails is shown in Figure 14-15. The hairs in the longer winter coat are also hollow and crinkled, with an underfur that consists of very fine hairs that are about as numerous as the longer hairs (Figure 14-16).

Coat color is a genetic characteristic of interest in analyzing the radiation exchange of an animal, especially because of seasonal changes in color, thickness, and depth. From a thermal point of view, it would be advantageous for an animal to have a dark coat in the winter so that a maximum amount of solar radiation could be absorbed. The infrared-radiation exchange is not related to the visible color of the coat, however. Many arctic animals are white in winter and dark in the summer, so other factors such as protective coloration must have had a greater influence on their genetic characteristics than did any thermal benefits from color. The slight differences in coat color of different ruminants in northern climates appear to have little relationship to the rigorous thermal regime.

Two ecological rules that relate body geometry to climate have become firmly entrenched in the ecological literature. Bergman's rule states that northern members of a species have a larger body size than southern members. This is inter-

FIGURE 14-15. The physical depth (cm) of winter hair at several points on white-tailed deer. (From Stevens 1972.)



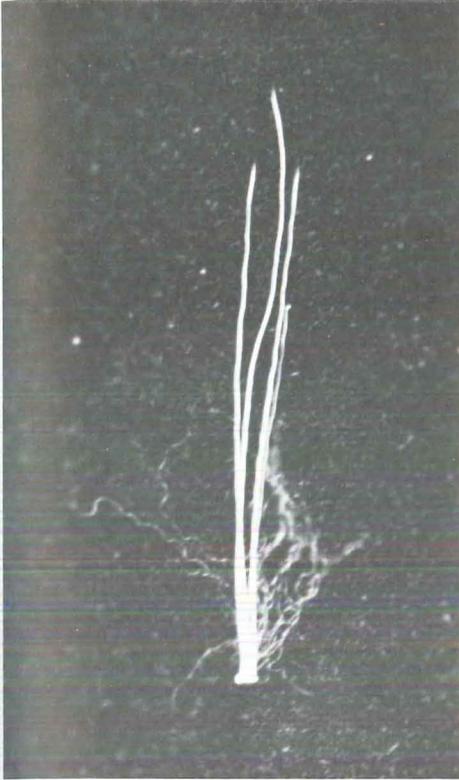


FIGURE 14-16. The long, guard hairs and the fine underfur of the winter coat of a white-tailed deer.

preted as a genetic adaptation to cold since a larger body has a higher volume-to-surface-area ratio than a smaller one. Allen's rule states that northern species have smaller appendages than southern ones. This is interpreted as an adaptation for the conservation of heat in the north with less surface area on legs and ears, and for the dissipation of heat in southern climates as the appendages act as cooling fins.

Several ecologists have recently questioned the validity of interpreting Bergman's rule on the basis of a climatic gradient. The rule is logical in theory, but the number of factors participating in thermal exchange and the compensatory effects of interaction between physiological and behavioral factors indicate that differences in body size are quite insignificant compared with other thermoregulatory mechanisms. Further, the younger members of each species are usually smaller than the mature animals in either north or south, so the rule is violated by each individual during its life span.

The functional basis for rules such as Bergman's can be successfully analyzed using a thermal-engineering approach. Work at the BioThermal Laboratory has indicated that differences in body size do appear to be significant but that deer seem to have other behavioral and physiological capabilities that compensate in part. Wathen, Mitchell, and Porter (1971) have studied the energy exchange of jackrabbit (*Lepus californicus*) ears, using both field and laboratory techniques.

Convection from the ears was large enough to account for the dissipation of all of the animal's metabolic heat production at an air temperature of 30°C, indicating that genetic adaptations such as large appendages may play a significant role in the maintenance of homeothermy.

14-7 SUMMARY

Careful analyses of energy relationships between an animal and its environment result in the conclusion that animals in northern climates are quite able to survive periods of cold weather if they can exhibit metabolic responses for the release of heat energy from ingested food or body tissue and physiological and behavioral responses for the conservation of heat energy. An adequate supply of energy and other nutrients is necessary for basal metabolic processes, for growth, and for production. The assimilation of nutritive considerations into a large ecological consideration of the concept of carrying capacity reveals some very interesting relationships, especially with respect to the importance of the characteristics of different age and weight classes within a population. This is discussed in Part 6.

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