Thermal Biology of Domestic Animals

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Abstract

The thermal environment is the most important ecological factor determining the growth, development, and productivity of domestic animals. Routes of energy exchange (sensible heat and latent heat) between animals and their environment are greatly influenced by body weight, fat deposition, hair-coat properties, functional activity, and number of sweat glands, as well as the presence or absence of anatomical respiratory countercurrent heat exchange capability. Differences in these anatomical features across species have led to specialization of heat exchange. Thermal plasticity and degree of acclimation are critical factors determining the ability of animals to respond to environmental change. Increases in productive capability of domestic animals can compromise thermal acclimation and plasticity, requiring greater investments in housing systems that reduce variability of the thermal environment. The combination of steadily increasing metabolic heat production as domestic animal productivity increases and a rising world temperature poses ongoing and future challenges to maintaining health and well-being of domestic animals.

INTRODUCTION

Thermoregulation is a neural process that connects information from the external environment to an appropriate efferent response (e.g., vasoconstriction, piloerection, panting), which permits the animal to maintain a stable internal environment relative to a variable external environment (1). These efferent autonomic pathways also provide the connection between the external environment and cellular metabolism by directly regulating transcription factors and indirectly regulating endocrine system activity (2). Although routes of energy exchange (sensible heat and latent heat) are fixed, variability among animals in body size, fat deposition, pelage, functional activity, and number of sweat glands, as well as the presence or absence of anatomical respiratory countercurrent heat exchange capability, has led to specialization of heat exchange among domestic animals; some use conductive energy exchange (swine) or respiratory exchange (ruminants, poultry), whereas horses have extremely high evaporative cutaneous heat loss. The steady increase in productive output of domestic animals has resulted in reduced plasticity of thermoregulatory responses to heat. Availability of new genomics tools now permits the opportunity to improve thermoregulatory plasticity in high-producing animals.

ROUTES OF HEAT EXCHANGE BETWEEN AN ANIMAL AND ITS ENVIRONMENT

All processes of life, all physiological events, do work and spend energy. A continuing supply of energy is necessary for an animal to live or maintain itself. One of the primary means by which the environment influences animals is through the exchange of energy. If the animal takes in more energy than it gives out, it will get warmer, overheat, and possibly die. If the animal loses more energy than it gains, it will cool and will not survive. An animal may warm or cool for a limited period of time, but on average, over an extended period of time, an animal must be in energy balance with its environment. For survival, maximum growth, and reproduction, animals need an environment most compatible with their physiological requirements for energy.

Livestock regulate their core body temperature, from approximately 38°C for cattle and swine to approximately 41.5°C for poultry, when exposed to a wide range of ambient temperature extremes. Core body temperature is maintained constant through a wide range of ambient temperatures, in part by adjusting metabolic heat production. Given the rich diversity in thermoregulatory strategies within mammals and birds, this section focuses more on cattle. The different routes of heat exchange between an animal and its environment are described below.

Sensible Heat Exchange

Animals lose heat in the form of sensible heat and latent (evaporative) heat. The driving force for sensible heat is temperature difference (gradient), that is, when the temperature of the animal is higher than that of the ambient for the animal to lose heat. Sensible heat loss occurs through three venues: conduction, convection, and radiation. Increasing ambient temperature lowers the temperature gradient between the animal and air and consequently decreases the sensible heat loss. Either radiation or convection can be a heat gain when ambient temperatures are greater than surface temperatures.

Conduction heat transfer occurs by direct contact of two surfaces; therefore, it is a molecular mode of heat transfer. Energy (heat) is exchanged from higher temperature to lower temperature. For a standing animal, the heat loss by conduction would be very small because the surface area in contact is negligibly small. When an animal is lying down, the contact area with the ground is approximately 20% of the total surface area (3). Cows are, however, more likely to stand in sunlight than to lie down because their body temperature increases when lying down owing to reduced effective surface area exposure for convective evaporative cooling (4).

For heat-stressed poultry, cool perches offer an effective method for conductive cooling. High blood flow rates to the uninsulated feet are possible because of the abundance of arteriovenous anastomoses, which bypass the capillaries between the arterioles and venules of the toes and contribute to 63% of the total blood flow at a high ambient temperature of 35.8°C (5). Cool (20°C ambient temperature) perches in a hot environment (35°C ambient temperature) prevented chickens from initiating panting, whereas chickens without the cool perches panted vigorously (6). Heat loss to cool perches ranged from 0.7 to 5.1 W per bird (7). At 35°C ambient temperature, broiler hens spent 62% of total perch time on water-cooled perches (20°C ambient temperature) and only 38% of perch time on air-equilibrated perches (8). Broilers raised in commercial pens with water-cooled perches had higher daily gains than broilers without the water-cooled perches (9), and performance of layers improved during periods of heat stress (10). Pigs prefer to spend more time lying in a wallow of water than standing, walking, or sitting in the wallow as ambient temperature rises (11). Mud continues to cool the pig nearly an hour longer than wetting alone because the mud holds more water than the skin surface can retain when simply wetted (12).

The equation describing conductive heat transfer can be simplified as follows:

$$q''_{cond} = k(\overline{T}_{skin} - T_{air}),$$

where q''_{cond} is the flux of conductive heat exchange, k is the thermal conductivity of the material in contact with the skin, $\overline{T}_{skin}$ is mean skin temperature, and T_{air} is air temperature.

Convection heat loss from a cow occurs by fluid (air) flowing over the surface of the animal. Again, convection is driven by the temperature gradient between the body of the animal and ambient air. Increasing ambient temperature lowers the temperature gradient between the animal and air and consequently decreases the sensible convection heat loss. Heat loss by convection could be free (natural) or forced convection. Free convection occurs when temperature difference in the boundary layer of air surrounding the animal causes a movement of the air in response to changes in air density caused by temperature difference. Forced convection occurs when external pressure difference causes air to blow past the animal. Forced convection is normally associated when mechanical systems (fans) are used in creating the external pressure. For example, increasing air velocity between 0.5 and 3.0 m/s over a cow's surface would increase convective heat loss by decreasing the insulation value of the boundary layer, or by reducing the insulation value of the hair coat if the velocity is greater than 3.0 m/s (13). Higher velocities penetrate into the hair coat and thus increase the convective heat loss from the fur layer and skin surface. The hair coat traps air, and air, being a poor conductor of heat, insulates the skin surface from losing heat during cold seasons.

The equation describing convective heat transfer can be expressed as follows:

$$q''_{conv} = h_c(\overline{T}_{skin} - T_{air}),$$

where q''_{conv} is flux of convective heat exchange, h_c is the convective coeffecient, $\overline{T}_{skin}$ is mean skin temperature, and T_{air} is air temperature.

Radiation heat exchange occurs between two surfaces as each surface emits energy at wavelengths that are dependent on the temperature of the emitting surface. Several thermal radiation sources in the surroundings of an animal can be mentioned, for instance, the sun, sky, ground, shelter (walls and roof), or buildings—in short, any object or surface, real or virtual, with a temperature above absolute zero (0 K or −273.15°C). To quantify the thermal radiation exchanged between an animal and its environment, the great complexity of the latter must be reduced to the conditions of a standard surface. Suppose an animal is placed in the center of an infinitely large spherical container, the inner surface of which is a black body at a mean radiant temperature. This temperature is the average temperature of all the surfaces that exist around the body of an animal in a given place. Such an animal exchanges with all those surfaces an amount of thermal energy known as radiant heat load, which can be defined as the total amount of thermal energy a body exchanges by radiation with its environment (14).

Either radiation or convection can be a heat gain when ambient temperatures are greater than surface temperatures. For example, chickens gained approximately 2 W of radiant heat and approximately 5 W of convective heat at an ambient temperature of 40°C and an air velocity of 2 m/s (15). Higher air velocity over chickens at 32°C or 36°C reduced respiratory evaporative heat loss owing to the effectiveness of convective cooling in lowering the need to pant (16).

When exposed to direct solar radiation, tropical Merino sheep lose 74% of their total evaporative heat loss through the skin. Likewise, Bedouin goats can lose 68% of the total evaporative heat through the skin under solar radiation at 30°C ambient temperature. Without solar radiation and at higher air temperatures (46°C), these Bedouin goats lose 50% of their evaporation through the skin (17). White Zebu steer can lose 97 $g/(m^2 \cdot h)$ from the skin of their backs exposed to direct sunlight, whereas the shaded skin of the belly loses half this amount (18). Donkeys, like horses, have always been known to be sweating ungulates. When exposed to the sun, donkeys can lose 240–360 $g/(m^2 \cdot h)$ from the skin, whereas in a hot laboratory, shielded from sunlight, they lose 170–200 $g/(m^2 \cdot h)$ (19).

For a small, convex object having emissivity ε at a temperature of $T_{surface}$ exchanging heat with much larger surroundings, all at the same temperature, T_{surr}, the radiative heat exchange is then given by

$$q''_{rad} = \varepsilon\sigma(T^4_{surface} - T^4_{surr}),$$

where q''_{rad} is the flux of radiative heat exchange and σ is the Stefan-Boltzmann constant. Infrared radiation refers to radiation of wavelengths longer than those in the visible portion of the spectrum.

Latent Heat Exchange

Sweating and panting are two of the primary autonomic responses exhibited by animals under heat stress. Cows and horses are considered sweating animals, although they supplement sweating with panting. Pigs and sheep are considered panting mammals, although wallowing for pigs and sweating for sheep can be major avenues of heat loss during extreme heat stress. Among livestock, poultry are the best examples of true panting animals. Sweating results in increased evaporative heat loss from the skin surface, whereas in panting, sensible heat from the body core is used to heat the water vapor and expel heat in the form of vaporized moisture from the lungs. However, these responses are likely driven more by skin temperature than by core body temperatures. Evaporative heat loss from skin and the respiratory tract is highly correlated with skin temperature. In fact, skin temperature is more highly correlated with these parameters than core temperature, suggesting that thermal receptors in the skin initiate the autonomic systemic response to thermal stress.

Cutaneous heat loss. Cattle use various behavioral and autonomic thermoregulatory mechanisms to relieve heat stress. An animal under heat stress may seek shade, change its orientation to the sun, and increase water intake (20). Sweating and panting are two of the primary autonomic responses exhibited by cattle under heat stress. Sweating results in increased evaporative heat loss from the skin surface. The driving force for cutaneous evaporative heat loss is a moisture gradient between the skin surface and ambient air. The animal loses sensible heat, which is used to evaporate the moisture on the skin surface, thus alleviating heat stress. At low ambient temperature, the animal is not sweating; thus, evaporative heat loss represents a very small fraction of metabolic heat production. When air temperature is between 10°C and 20°C, heat loss by cutaneous evaporation accounts for 20–30% of the total heat loss, but when the temperature is greater than 30°C, cutaneous evaporation becomes the dominant mode of heat loss, accounting for approximately 85% of the total heat loss, and the rest is lost by respiratory evaporation (21). For the casual observer, this may be surprising, because panting is easily observed in heat-stressed cows. However, droplets of water on the skin are visible only under a stereomicroscope and not to the naked eye (22, 23). When animal surface temperature equals ambient temperature, sensible heat loss is zero because there is no temperature gradient, and evaporative heat loss via sweating and panting becomes the only available venue for the animal to lose heat. Both sweating and panting, however, have the undesirable side effect of depleting body-water reserves.

Horses have the highest sweating rates of any endotherm, approximately double the maximum sweating rates of humans. Sweating rates as high as 2,400 g/(m^2·h) have been measured in exercising horses galloping at speeds of 10 m/s (24). This reported study is one of many studies in which maximal sweating rates of horses are induced by exercise rather than by exposure to heat stress. The aforementioned study was conducted in a laboratory with ambient temperatures between 21.0°C and 23.5°C where the contribution of cutaneous and respiratory evaporative heat loss to the total evaporative heat loss was approximately 71% and 29%, respectively. Only approximately one-third of the 2,400 g/(m^2·h) lost by sweating contributed to evaporative heat loss because most of the water dripped off from the skin surface, rendering it useless for evaporative heat loss.

Goats and sheep have lower sweating rates than cattle. At 42°C ambient temperature and 14% relative humidity, adult goats sweat at 212 g/(m^2·h), compared with 70–112 g/(m^2·h) for adult, unshorn sheep (25). In Corriedale sheep, approximately 63% of total evaporative heat loss is cutaneous, and the remainder is from the respiratory passages (26). Pigs evaporate approximately 30 g/(m^2·h) from the skin by passive diffusion when exposed to 29°C and a relative humidity of 90%, and this represents 67% of the total evaporative heat loss (27). The evaporative critical temperature for pigs panting ranges from an ambient temperature of 21°C (28) to 30–32°C (29). Chickens can dissipate 170% of metabolic heat production at 45°C ambient temperature from panting evaporative heat loss (30). Although panting is an effective mechanism for evaporative heat loss, it does have a deleterious side effect, respiratory alkalosis.

The driving force for moisture production seems to be skin temperature (31). Cutaneous evaporation is affected by air velocity, ambient temperature, relative humidity, and thermal and solar radiation. Air velocity (or wind) greatly increases evaporative heat loss from the skin surface by penetrating the hair coat and thus reducing the effective thickness of the hair coat, which acts as insulation (32). Within the hair coat, thermal resistance decreases linearly with increasing air velocity. Increasing air velocity over the hair-coat surface from approximately 0.2 m/s to approximately 0.9 m/s raised water evaporation rates from approximately 75 g/(m^2·h) to approximately 350 g/(m^2·h), and no further increase occurred when air velocity was increased to 2.2 m/s (33). A rise in relative humidity from 30% to 90% lowers sweating rate from approximately 500 g/(m^2·h) to approximately 60 g/(m^2·h) (34). Collier et al. (35) developed an empirical equation for calculating sweating rate [j''_{sr} = flux of water vapor that evaporates from the skin surface, g/(m^2·h)] as a function of skin temperature, which is expressed as

$$j''_{sr} = 1.1665^{*}T_{skin}^{2} - 64.166^{*}T_{skin} + 894.35 \quad \text{if } T_{skin} < 35°\text{C}$$

$$j''_{sr} = 4.2976^{*}T_{skin} - 71.289 \quad \text{if } T_{skin} \geq 35°\text{C}.$$

Jiang et al. (36) provided a fundamental but more complex equation for flux of water vapor that evaporates from the skin surface. Once the sweating rate or flux of water vapor is known, the heat flux lost by evaporation (q''_{evap}) can be calculated by

$$q''_{evap} = \lambda j''_{sr} \beta,$$

where λ is latent heat of evaporation of water at temperature of skin surface (kJ/kg) and β is percent of wet skin surface area owing to sweating.

Other factors that affect the efficacy of evaporative cooling of the skin surface are physical properties of the hair coat, such as hair density, hair length, and hair-coat thickness. High hair-coat density, which is necessary in cold weather to provide insulation by trapping air, becomes an obstruction to free evaporation of water from the skin surface in hot weather (37). Hair diameter and hair-coat thickness have similar effects, resulting in heat stress of the animal in hot weather. Thicker hair coats resist evaporative heat loss more than thinner hair coats do (38), which is consistent with the observation that resistance to the diffusion of water vapor through a hair coat is similar to the diffusion resistance for still air of equivalent thickness (39). Hair and skin color, if black, enhance solar absorption and thus increase the solar heat load on the skin surface. The process of evaporative cooling is a complex interaction of humidity and temperature difference between air and skin, air velocity, and hair-coat characteristics, such as density and depth.

Cutaneous moisture production (sweating rate) ranged between 189 ± 84.6 g/(m^2·h) and 522 ± 127.7 g/(m^2·h) for a solar load exposure greater than 500 W/m^2 (average 833 ±132 W/m^2), average temperature-humidity index of 82.7 ± 1.64, air velocity between 0.8 m/s and 1.2 m/s, and body (rectal) temperature greater than 38.8°C (threshold for heat stress) (37). The same report indicated that in a hot and dry environment, evaporative cooling was profoundly increased [from 68 g/(m^2·h) before wetting to 508 g/(m^2·h) after wetting the skin surface with water, exposed to 0.2 m/s air velocity, and without solar load], and the rate was further increased [from 296 g/(m^2·h) before wetting to 961 g/(m^2·h) after wetting] when air velocity over the wetted skin surface was increased to 0.9–1.0 m/s. In a hot and humid environment, however, the increase was relatively modest [from 258 g/(m^2·h) before wetting to 490 g/(m^2·h) after wetting] for an air velocity of 0.9–1.0 m/s and a solar load greater than 600 W/m^2. Moisture production is higher in hot and dry conditions than in hot and humid conditions because of the higher moisture gradient between the skin surface and ambient air. Unless a cow is in a very hot and humid climate, it is reasonable to assume that all the sweat it produces will evaporate. In other words, the sweating rate equals the evaporation rate at low humidity. However, as the relative humidity increases, the evaporative rate will decrease, and the mass flux decreases linearly as the humidity of the air increases (40).

A prolonged (extended) exposure to hot and dry conditions or exposure to 3 h of 850 W/m^2 of solar load caused rectal temperature to rise above 40.0°C and respiration rate to rise above 125 breaths/min. Under these conditions, black or predominantly black cows were observed foaming in the mouth, sticking their tongues out, and drooling (31). During these events, immediate intervention with water spray on the body helps to alleviate heat stress. A physiological upper limit of moisture production, which is different for each cow, seems to exist. The maximum sweating rate measured was 660 g/(m^2·h) for dairy cows and feedlot heifers (31).

Sweating moistens the skin surface and usually leaves the hair-coat layer dry. Wetting the hair coat with a mist of water adds water to the coat surface and penetrates deep down to the skin surface and wets it. Wetting the hair coat is a more effective means of losing heat than sweating (40). Hillman et al. (41) reported that heat-stressed cows actively stand under water spray to wet their hair coat. Wetting the hair coat and the skin surface lowers the core body temperature, and causing a faster drop in core body temperature by spraying water at short time intervals (such as

10 min) greatly enhances evaporation rate. Increasing wind speed over the hair coat further speeds up the rate of evaporation (42, 43).

Respiratory heat loss. Panting is a controlled increase in respiratory frequency in concert with a decrease in tidal volume, which increases ventilation of the upper respiratory tract while preserving alveolar ventilation. The increase in upper respiratory tract ventilation increases evaporative heat loss (44). Panting appears to be under an independent control and is more highly correlated with surface than with core temperature (35). The water in the inspired air comes in at an ambient temperature and pressure. The expired air comes out at body temperature and is saturated. Therefore, energy is expended to vaporize the water within the respiratory tract. The amount of water lost in grams per unit of time when multiplied by the latent heat of vaporization of water at the appropriate temperature gives the rate of water loss in energy units. In other words, sensible heat is used to heat the water vapor and remove heat in the form of vaporized moisture from the lung. According to Maia et al. (34), the onset of panting (i.e., the evaporative critical temperature) occurs at approximately 19°C.

Although increases in ventilation during panting are mostly limited to dead space, there is a detectable increase in alveolar ventilation because dead space ventilation cannot be effectively separated from ventilation of the alveolar units. If evaporative heat loss is insufficient and body temperature rises, the respiratory pattern changes and tidal volume increases, whereas respiratory frequency decreases and animals switch from closed- to open-mouth respiration. The resulting alveolar hyperventilation leads to a progressive development of a marked respiratory alkalosis, which has health consequences (44–46).

The equation for calculating the heat flux lost by respiratory evaporation is expressed as (47)

$$q''_{resp} = \frac{\lambda VF\left(\omega_{exp} - \omega_{air}\right)}{60A},$$

where λ is $2500.7879 - 2.3737^*$; t_{air} is the latent heat of vaporization (J/g); V is tidal volume (m^3/breath); F is respiratory rate (breaths/min); ω_{exp} and ω_{air} are absolute air humidity of the expired and atmospheric air, respectively; A is body surface area; and t_{air} is air temperature (°C).

The absolute air humidity values are calculated as

$$\omega_{\mathrm{exp}} = \frac{2166.87^* P_p\left\{t_{exp}\right\}}{273.15 + t_{exp}}$$

$$\omega_{air} = \frac{2166.87^* P_p\left\{t_{air}\right\}}{273.15 + t_{air}},$$

where $P_p\{t_{exp}\}$ and $P_p\{t_{air}\}$ are the partial vapor pressures (kPa) of expired and ambient air, respectively, and t_{exp} and t_{air} are temperatures (°C) of expired and ambient air, respectively.

Modeling Heat Exchange Between an Animal and the Environment

The exchange of energy between an animal and its environment affects the body temperature of the animal. Body temperature, including skin surface temperature and hair-coat-layer temperature, depends on environmental factors. The rate of water loss, both cutaneous and respiratory, is determined in part by environmental conditions and in part by the animal's physiology. The environmental factors that are primarily responsible for energy flow to an animal are air temperature; sky temperature; solar and infrared radiation; wind speed and humidity; and geometric structural properties of animal hair coat, such as hair-coat density, hair diameter, hair-coat thickness, and hair-coat and skin color, which influence solar absorptivity and transmissivity. The microclimate surrounding an animal can be thought of as a four-dimensional space in which the four independent environmental variables—radiation, wind speed, air temperature, and relative humidity—are acting simultaneously and are each time dependent.

It is difficult, if not impossible, to describe mathematically all of the dynamic thermal relationships between an animal and its thermal environment in its natural habitat. It is obviously impractical to examine experimentally all the possible combinations of radiation, air temperature, wind velocity, relative humidity, animal size, metabolic rate, evaporative and respiratory water losses, and hair-coat physical and optical or spectral properties. There are considerable experimental difficulties in measuring accurately animal thermal responses in their natural habitat. Therefore, mechanistic models must be developed to simulate the energy exchange between the animal and its environment and to evaluate and predict outcomes of interactions of environmental variables and animal parameters.

Cattle, like any other endotherm, are considered to be homeothermic; i.e., they maintain constant body temperature over a wide range of environmental extremes. This, of course, is not absolute, there being a diurnal fluctuation. Homeothermy requires that the amount of heat produced or gained from the environment must equal the heat lost to the environment, as indicated by the following equation:

$$M = \pm q''_{cond} \pm q''_{conv} \pm q''_{rad} + q''_{evap} + q''_{resp}\,,$$

where M is metabolic heat production. Heat loss is directly related to metabolism and, therefore, to feed requirements for survival, production (or growth), and reproduction potential.

For an animal in complete thermal equilibrium, there will be no change in heat storage; however, at any one instant in time there is never a complete balance, and a value for rate of heat storage can be added to the equation, recognizing that this would be a non-steady-state condition. The heat exchange by conduction, convection, and radiation has a plus and minus sign opposite it; i.e., heat can be gained by these means as well as lost. Heat exchange by cutaneous and respiratory evaporation is usually away from the animal and therefore always has a plus sign.

Mathematical models have been developed for over 30 years to simulate the thermal interactions of animals and their environment. More recently, models have been refined as the heat and mass transfer relationships become better understood and as more measurements are collected on thermoregulatory responses and morphological characteristics of cattle (36, 48–53). These models examine the complexities of sensible and latent heat flow from the skin surface and hair coat where the cow interacts with its environment. It should be noted that the climatic energy demands (food and water requirements) for a cow are a coupled heat and mass transfer problem and can be determined from an energy balance on the skin surface (48).

More fundamentally, the governing equation of heat flow through the hair coat for steady-state heat conduction with heat generation term can be expressed as

$$k_{eff}\frac{d^2T}{dx^2} + q'''_{sol} = 0,$$

where k_{eff} is the effective thermal conductivity of the hair coat and q'''_{sol} is the volumetric heat-generation term within the hair coat owing to absorption of solar radiation. The following boundary conditions are needed to solve the equation: (*a*) At the hair coat–air interface, the conduction term is equal to the convective term, and (*b*) at the skin surface, the skin temperature is either estimated or calculated. The two boundary conditions can be mathematically expressed as at the hair coat–air interface ($x = 0$): $k_{eff}\dfrac{dT}{dx} = h_c(T - T_{air})$, and at the skin surface ($x = d$): $T = T_{skin}$, where h_c is the convective heat transfer coefficient at the interface of the hair coat and ambient air. The effective conductivity, k_{eff}, in the conduction term accounts for the physical properties of the hair coat, and d is the depth of the hair coat.

The mathematical formulation for the above indicated model is for a steady-state situation. However, much of the time, an animal is in a transient energy state as it moves about in the environment. While in transient states, the energy budget for an animal must average within the environmental limits permitted by the steady-state requirements for survival. The basic concept is of a one-dimensional heat transfer model through the animal's hair coat, and the solution provides the temperature profile through the hair coat. The model is a function of environmental parameters and hair-coat physical properties. The absorbed solar radiation within the hair coat is incorporated into the model as an internal heat-generation source. The model is developed from basic principles.

FACTORS AFFECTING HEAT EXCHANGE

Hair-coat properties are inputs to heat and mass transfer models of animals. It is therefore imperative that physical and optical properties of the hair coat are accurately characterized for modeling heat and mass transfer through the hair coat. Moreover, hair-coat properties can provide information on which breeds of animals are more likely to adapt to particular environments. Physical and optical data in the literature are sparse at best; what is available is mostly from studies done in the early 1950s to 1970s, which do not represent present-day high–milk volume–producing cows and changes in animal feed nutrition.

The hair coat of animals plays a critical role in heat and moisture transfer from the skin surface to the surrounding environment and body temperature control. Endotherms interact with the thermal environment that affects their growth, production, and reproduction potential at the skin–hair coat interface (54). The animal hair coat traps air to provide insulation from cold but becomes an obstruction for evaporative cooling by reducing the velocity and moisture gradients through the fur layer in hot and humid conditions (54). When an animal is exposed to sunlight, a temperature gradient is formed between the hair-coat surface and the skin (55). The hair coat is one of the most significant factors that affect the heat-dispersion rate from the body to the environment (56).

The hair coat provides insulation not only from the cold but from heat as well. It tends to ameliorate the thermal regime of the body proper by buffering the thermal variations. The directional pile of bird feathers allows less wind penetration and greater heat resistance when the wind follows the natural contours of the feathers than when it travels against it (57). The effect of direct solar radiation on the radiant temperature over the entire surface of an animal is not uniform because both the color of this surface and the angle of the rays striking the surface are important in determining just how much solar energy is absorbed.

In a study on the effect of hair color on thermoregulation, Hillman et al. (43) reported that when black Holstein cows were exposed to direct sunlight, their surface temperature increased by 4.8°C, and that of white cows increased by 0.7°C. The difference in temperature between black and white is because of higher solar absorption by black than white. They also reported that rectal temperature increased at a rate of 0.7°C/h for black cows and 0.3°C/h for white cows. In another study, Hillman et al. (41) reported an increase in sensible heat flux in the order of 26% for dark-red, 22% for black, 5% for tan, and 4% for white cows.

Da Silva et al. (58) investigated radiative properties of the skin and hair coat of various breeds of cattle with respect to shortwave radiation. The study concluded that light-hair coats exhibited much higher reflectivity than dark-hair coats for wavelengths ranging from 300 nm to 850 nm. Façanha et al. (59) measured physical properties of hair coats of Holstein cows managed at Quixeramobim (latitude 5°30′ south and longitude 39°18′ west), Ceará State, Brazil, from June 2000 to March 2001. The hair-coat thickness was measured at black spots at the center of the thorax approximately 20 cm below the dorsal line. Hair samples were taken from the same area where the hair-coat thickness was measured. The hair samples were stored in plastic envelopes, and the measurements (hair length and hair density) were made in the laboratory. Hair length was given as the mean length of the longest ten hairs of each sample. The number of hairs per unit area was estimated by directly counting all the hairs of each sample.

Compilations of physical and spectral properties of the hair and hair coat of cattle from the recent literature are given in **Tables 1** and **2**, respectively. It should be noted that the physical properties vary with body location and climate. For example, cows shed their hair during the summer.

THERMAL ENVIRONMENT AND METABOLISM

The functions of thermoregulation and cellular metabolism are dissociated in ectotherms, which limits their ability to alter metabolism in response to the thermal environment, other than redistribution of cardiac output. However, the thermal environment has a large impact on the metabolic rate of ectotherms through Q_{10} effects. Ectotherms largely regulate their body temperature through behavioral means, as well as cardiovascular regulation of heating and cooling (60). Endotherms, which include all domestic mammals and birds, combine these two functions (thermoregulation and cellular metabolism), and it is cellular metabolism in endotherms that generates the heat required for adaptive thermogenesis (2, 61). The two pathways linking sensing of environmental change and acclimation in ectotherms may be similar to those pathways linking thermal signals to thermal regulation in endotherms (2). These two pathways are the autonomic sympathetic nervous system and the endocrine system.

Under thermoneutral (condition of least thermoregulation) conditions, basal metabolism is unrestricted and is based on body mass. Under these conditions, metabolic rate associated with productive functions will reach genetic capacity if sufficient nutrients are available. In domestic animals selected for high productive capacity, this requires partitioning of nutrients toward productive functions, which is under homeorhetic control (62). When an acute environmental stress is applied to this system, net energy for production must be diverted to meet the increased energy demand for maintenance requirements. Activation of the autonomic nervous system by acute stress is associated with reductions in feed intake and losses in productivity, redistribution of cardiac output, increased evaporative heat loss, and activation of the heat shock response at the cellular level (46, 63). When the stress persists, animals undergo reprogramming of gene expression and display altered sensitivity to homeostatic signaling, along with increased efficiency of metabolic pathways (64). These changes are termed acclimation and have been shown to be a subcomponent of the homeorhetic control of metabolism (62, 65). Acclimation is regulated by the endocrine system and requires a longer response time than the acute phase response to an environmental challenge. Thus, the two pathways (the autonomic sympathetic system and the endocrine system) represent the pathways for both acute and chronic responses to environmental change.

Acute Metabolic Response to Thermal Stress

Activation of the acute response to thermal stress is initiated by a subfamily of the transient receptor potential (TRP) ion channel superfamily. These thermo-TRP gated ion channels exist on free nerve endings of somatosensory neurons located in the dermis and epidermis, and different

Table 1 Physical properties of hair and hair coat of cattle[1]

Breed	Hair length (mm)	Hair diameter (µm)	Hair-coat density (mo/cm^2)	Hair-coat depth (mm)	Study location	Comments
Holstein (Rump)[2]	21.62 ± 2.93 (85)	48.80 ± 9.09 (21)	5200 (at skin level)	12.35 ± 1.29 (13)	United States (Wisconsin)	Winter
Holstein (Lumbar)	22.05 ± 3.69 (86)	54.97 ± 9.27 (19)	7200 (at skin level)	14.16 ± 1.08 (15)	United States (Wisconsin)	Winter
Holstein (belly ventral)	21.04 ± 5.02 (67)	41.66 ± 10.75 (28)	6300 (at skin level)	15.28 ± 1.97 (15)	United States (Wisconsin)	Winter
Holstein (thoracic lateral)	17.13 ± 2.68 (62)	41.73 ± 8.03 (26)	6250 (at skin level)	10.55 ± 1.41 (15)	United States (Wisconsin)	Winter
Holstein (Head)	18.40 ± 3.12 (79)	43.70 ± 7.30 (28)	3900 (at skin level)	12.56 ± 1.76 (15)	United States (Wisconsin)	Winter
Holstein (grand total)	20.05 ± 3.49 (399)	46.375 ± 10.7 (245)	3900–7200 (at skin level)	12.98 ± 2.23 (73)	United States (Wisconsin)	Winter
Holstein[3]	12.60 ± 3.45	62.49 ± 5.6	987.00 ± 347	2.48 ± 0.48	Brazil	Tropical climate
Braford[4]	10.41 ± 3.91	30.98 ± 8.13	993.18 ± 503	3.73 ± 1.72	Brazil	Tropical climate
Gyr (Zebu)[5]	4.68 ± 1.22 (15)		1140.62 ± 289 (15)	2.68 ± 0.34 (15)	Brazil	Tropical climate
Zebu × 50–75%	6.81 ± 1.81 (28)		971.62 ± 292 (28)	2.68 ± 0.47 (28)	Brazil	Tropical climate
Holstein						
Zebu × >75%	8.74 ± 2.22 (31)		1071.90 ± 237 (31)	2.95 ± 0.44 (31)	Brazil	Tropical climate
Holstein						
Holstein[6]	11.1	40.1	1201	2.2	Brazil	Tropical climate
Brangus	20.8	41.2	867	2.4	Brazil	Tropical climate

(*Continued*)

Table 1 *(Continued)*

Breed	Hair length (mm)	Hair diameter (μm)	Hair-coat density (mo/cm^2)	Hair-coat depth (mm)	Study location	Comments
Nelore	13.6	53.5	1944	3.2	Brazil	Tropical climate
Simmental	15.0	39.0	939	1.7	Brazil	Tropical climate
Canchim	17.1	47.0	1206	1.9	Brazil	Tropical climate
Holstein[7]	12.02 ± 0.14		1552 ± 25	1.93 ± 0.086	Brazil	Tropical climate

[1] Values given are mean and standard deviation (numbers in parentheses are sample sizes).

[2] Gebremedhin et al. (48).

[3] Bertipaglia et al. (55).

[4] Bertipaglia et al. (96).

[5] Verissimo et al. (97).

[6] da Silva & Starling (26). Values are averaged for the same breed but different colors.

[7] Façanha et al. (59).

Table 2 Spectral properties of hair coat of cattle

Breed	Hair color	Absorptivity	Reflectivity	Transmissivity	Study location
Angus[1]	Black	0.98			United States
MARC III	Dark Red	0.92			United States
MARC I	Tan	0.75			United States
Charolais	White	0.37			United States
Holstein[2]	Black	0.89 ± 0.01			United States
Holstein	White	0.657 ± 0.045			United States
Holstein[3]	Black	0.902	0.0893		Brazil
Holstein	White	0.518	0.4536		Brazil
Holstein[4]	Black	0.93	0.06	0.01	Brazil
Holstein	White	0.43	0.53	0.04	Brazil
Holstein	Red	0.37	0.44	0.19	Brazil
Brangus	Black	0.92	0.07	0.01	Brazil
Nelore	Dark Gray	0.91	0.04	0.05	Brazil
Simmental	Red	0.54	0.29	0.17	Brazil
Canchim	Gray	0.27	0.66	0.07	Brazil

[1] Gebremedhin & Wu (52).
[2] Hillman et al. (43).
[3] Maia et al. (34).
[4] da Silva & Starling (26).

members have different thresholds of temperature activation (66). It is generally accepted that core body thermoreceptors, because they lie deep within the body and cannot sense changes in environmental temperatures, do not contribute to thermal responses to the environment unless the temperatures are extreme (67). Six thermo-TRPs have been described to date: TRP vanilloid (TRPV) 1 and 2 are activated by noxious levels of heat, TRPV3 and 4 respond to nonnoxious warmth, TRP melastatin 8 is activated by nonnoxious cool temperatures, and TRP ankyrin 1 is activated by noxious cold (68). The cell bodies for TRP neurons lie in the dorsal root and trigeminal ganglia. Thermal information is sent from thermal TRP neurons and travels up lamina-I neurons via the spinothalamic tract to the thalamus and then to the preoptic area of the hypothalamus and the anterior hypothalamus (**Figure 1**) (69, 70). Sensory information also travels from the thalamus to the cerebral cortex for thermal perception (**Figure 1**). Efferent information from the hypothalamic centers is sent to the nucleus raphe pallidus of the medulla oblongata, which then activates sympathetic preganglionic neurons controlling thermoregulatory responses, such as cardiovascular responses, skin vessel vasodilation, or constriction and metabolic changes (71, 72). Sympathetic activation of the adrenal medulla can also cause release of catecholamines directly from the adrenal medulla, which can also modify cellular metabolism and vascular distribution. Therefore, efferent autonomic pathways are the common link between the thermal environment and metabolism at the cellular level, for both the acute and chronic responses to environmental stress (61). Transcription factors are key regulators of cellular metabolism, and several play

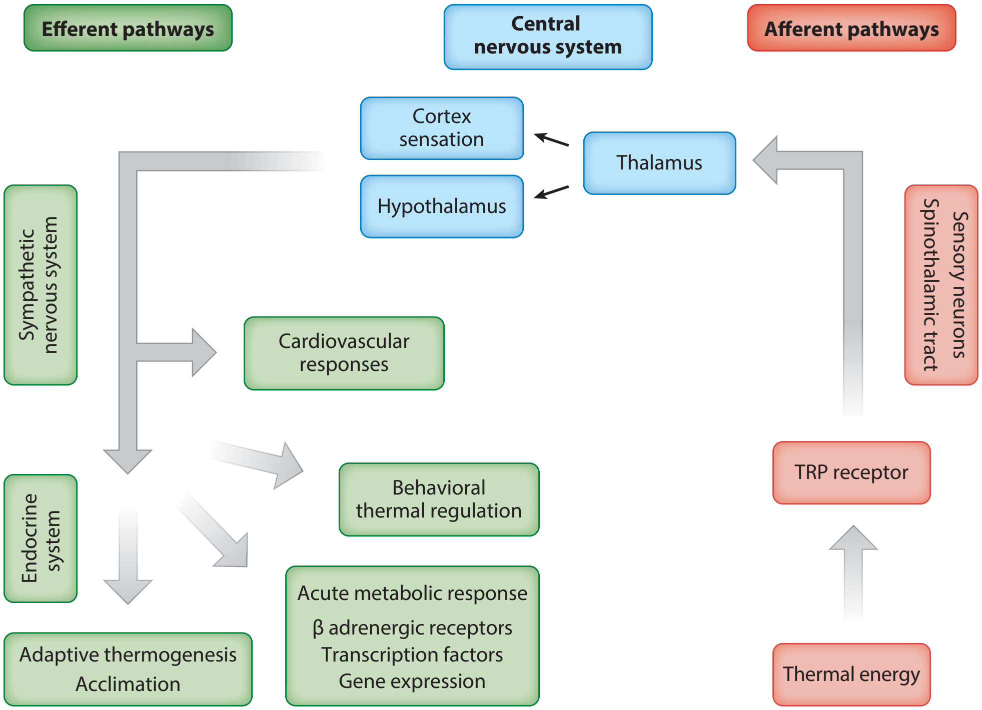

Figure 1

Afferent and efferent pathways in acute and chronic metabolic responses to thermal stress. Abbreviation: TRP, transient receptor potential.

important roles in the metabolic response to thermal stressors. Examples include peroxisome proliferator activated receptor γ coactivator 1α and β (PPARGC1α & β), hypoxia inducible factor 1 (HIF1A), and heat shock factor 1 (HSF1) (2, 73, 74). These transcription factors sit at the top of cascades that are initiated by thermal or oxidative stress (2, 75). As one example, HSF1 has now been shown to regulate up to 3% of the genome in yeast and has a regulatory impact on genes ranging in function from signal transduction to energy production, small molecule transport, carbohydrate metabolism, cytoskeletal organization, and vesicular transport (74). Immunolocalization and chromatin immunoprecipitation indicate that HSF1 binds to a similarly broad array of non–heat shock protein genes in human erythroleukemia cells (76). Activation of HSF1A is required for initiation of the cellular heat shock response, and HIF1A is required for heat acclimation (77, 78). There is also ample evidence now that acclimation to one stress (e.g., heat stress) leads to cross-tolerance to other stressors (e.g., oxidative stress) because both responses share the same cellular signaling regulatory pathways (79, 80).

Chronic Metabolic Response to Thermal Stress

When an environmental stress persists, the response to the stress moves from the acute phase to the chronic or acclimation phase. The end result of acclimation is to reduce the impact of the stress on the physiological system and to improve endurance and resistance to the temperature extreme (80). Baumgard & Rhoads (81) recently reviewed metabolic acclimation to chronic thermal stress.

They pointed out that domestic animals alter their metabolic and fuel selection priorities independently of nutrient intake or energy balance during acclimation to thermal stress. These alterations include a shift in carbohydrate metabolism, including changes in basal and stimulated circulating insulin levels. The production of glucose from liver and metabolism of glucose by muscle also demonstrate differences in glucose production and use during heat stress. The studies by Baumgard & Rhoads (81) also demonstrated an apparent lack of fat mobilization from adipose tissue coupled with a reduced responsiveness to lipolytic stimuli despite a pronounced negative energy balance, demonstrating marked changes in metabolic fuel availability during acclimation to thermal stress. Collectively, their work demonstrates that acclimation to heat stress is a homeorhetic process involving alteration of carbohydrate, lipid, and protein metabolism independently of reduced feed intake. Acclimation is mediated by coordinated changes in metabolic fuel supply and use by multiple tissues. This is a rapidly evolving area of thermal biology, and we do not yet understand the genomic regulatory process involved sufficiently to allow us to identify potential pathways to improve metabolic performance during environmental stress.

THERMAL PLASTICITY VERSUS ACCLIMATION

At latitudes where there are large seasonal changes in the thermal environment, animals anticipate these changes by undergoing seasonal changes in their phenotype (hair-coat thickness, pelage thickness, body fat). This response is termed plasticity if it involves morphological traits and acclimation if it involves physiological and metabolic traits (82). The effect of phenotypic plasticity is to improve the fitness of an animal in the altered environment.

Acclimation to thermal stress has long been the central focus of research by physiologists and nutritionists. However, there is very little available information on the impact of thermal plasticity on ability to acclimate to thermal stressors. For instance, it is generally recognized that *Bos taurus* cattle are less adapted to heat stress than *Bos indicus*, and *B. taurus* exhibits greater thermal plasticity with regard to cold stress. However, there is no published work on either the effect of thermal plasticity to cold, ability to adapt to heat, or the degree of genetic variation in plasticity within these genetic subgroups. Bernabucci et al. (46) have pointed out that within domesticated ruminants, differences exist between species, breed, and production level with regard to heat stress susceptibility as well as time required for acclimation and level of acclimation. Some of these differences are associated with production levels and feed intake. However, we do not know the role that thermal plasticity plays in these differences. These areas represent opportunities for future studies.

COSTS OF ACCLIMATION

Generally, the process of acclimation results in lower productive output of domestic animals, and this loss in production is more pronounced in higher-producing animals (83). For example, after acclimation to thermal stress, high-producing animals were unable to return to their former level of milk production, whereas lower-producing animals were successful in returning to prior levels of production (84). For this reason, large capital investments have been made by domestic animal industries to reduce the impact of the thermal environment on level of productivity and reduce the need for animals to undergo acclimation. This is especially true in confinement animal operations (dairy, swine, and poultry) because of the concentration of animals and subsequent heat load and in the dairy industry because of the metabolic heat output of today's high-producing dairy cows (85). Alternative feeding strategies to reduce impacts of thermal stress have been minimally successful (46). In addition, it is known that genetically heat-adapted animals are more heat tolerant because of lower levels of production and reduced heat output (83). For the near future, livestock producers will continue capital investments to reduce environmental effects on productivity. However, new information from ongoing research in genomics offers some hope for future gains in selective manipulation of domestic animal genomes to improve thermal tolerance while maintaining productivity.

Approaches to Genetic Manipulation of Thermal Adaptation

Genetic approaches toward improving thermotolerance have advanced most rapidly in plant agriculture (86), where genetic manipulation is more easily carried out. However, new biotechnology tools hold the promise of reducing the impact of heat stress on animal production. Some recent developments include identification and selection of genomic polymorphisms that confer improved resistance (87) and identification of genetic pathways controlling physiological and cellular processes involved in thermotolerance at the animal and cellular level (35, 81). Additionally, the prospect of using gene silencing and gene activation to improve thermotolerance has been proposed (88, 89), and the opportunity now exists to move specific genes that improve thermotolerance from one population to another through genetic selection and genetic engineering (88). Reproductive technologies hold the promise of speeding up genetic progress by reducing generation time and increasing our ability to rapidly propagate superior genotypes. Biotechnology can also facilitate maintenance of rare genotypes of livestock that contain sets of genes that could be important for enhancing adaptation to specific environments (88).

Several genome-wide association studies have now been carried out in cattle (90–92), and several candidate single-nucleotide polymorphisms and quantitative trait loci have been identified as associated with thermotolerance or thermosensitivity. Testing of these single-nucleotide polymorphisms is ongoing and will yield genetic markers for identification of thermal resistance or thermosensitivity in cattle. Other genes have been identified through in vitro studies (35), and some of these genes were also identified in genome-wide association studies (93). The discovery of the slick gene in cattle (94) and its impact on thermotolerance has underscored the importance of regarding the hair follicle and fiber and its associated sweat gland in cattle as a single unit that impacts cutaneous heat loss. This unit is where thermal plasticity (hair length and thickness) and metabolic activity of the sweat gland (acclimation) interact and impact thermal tolerance. The slick gene was discovered in Senepol cattle (94) and, because it displayed simple dominance, was relatively easy to incorporate into the Holstein breed through crossbreeding.

The discovery that the *uncoupling protein 1* gene (*UCP1*), which is required for thermogenesis in brown adipose tissue, is silenced in pigs (89) provides an explanation for the fact that piglets are behaviorally well developed at birth but have poor thermoregulatory ability. Piglets must rely on shivering as the main mechanism for thermoregulation (95). Activation of this gene would improve performance and survival of newborn piglets.

Collectively, these findings and many others make it clear that use of new biotechnological tools will provide opportunities for improving thermal tolerance of livestock. When combined with reproductive technologies, such as cloning, gender selection, and embryo transfer, it is clear that genetic progress in the decade ahead will be much more rapid than previously thought possible.

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