SCHOLARLY REVIEW

A review of thermal stress in cattle

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Cattle control body temperature in a narrow range over varying climatic conditions. Endogenous body heat is generated by metabolism, digestion and activity. Radiation is the primary external source of heat transfer into the body of cattle. Cattle homeothermy uses behavioural and physiological controls to manage radiation, convection, conduction, and evaporative exchange of heat between the body and the environment, noting that evaporative mechanisms almost exclusively transfer body heat to the environment. Cattle control radiation by shade seeking (hot) and shelter (cold) and by huddling or standing further apart, noting there are intrinsic breed and age differences in radiative transfer potential. The temperature gradient between the skin and the external environment and wind speed (convection) determines heat transfer by these means. Cattle control these mechanisms by managing blood flow to the periphery (physiology), by shelter-seeking and standing/lying activity in the short term (behaviourally) and by modifying their coats and adjusting their metabolic rates in the longer term (acclimatisation). Evaporative heat loss in cattle is primarily from sweating, with some respiratory contribution, and is the primary mechanism for dissipating excess heat when environmental temperatures exceed skin temperature (~36°C). Cattle tend to be better adapted to cooler rather than hotter external conditions, with *Bos indicus* breeds more adapted to hotter conditions than *Bos taurus*. Management can minimise the risk of thermal stress by ensuring appropriate breeds of suitably acclimatised cattle, at appropriate stocking densities, fed appropriate diets (and water), and with access to suitable shelter and ventilation are better suited to their expected farm environment.

Keywords acclimatisation; cattle; cold-stress; heat-stress; homeostasis

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This review examines cattle thermal homeostasis; how cattle respond to changes in thermal load, how responses can be measured, and risk factors that can lead to adverse changes in body temperature. Where possible, heat exchange within and between the body of cattle and the environment has been quantified. Our focus is on management interventions that reduce the risk of adverse changes in body temperature. Other reviews have focused on describing but not quantifying heat energy transfer rates.[1,2]

The movement of heat (energy) follows the laws of thermodynamics. Energy movement into/out of the body of cattle will be quantified where possible to aid in the understanding of the magnitude of impacts and the potential effectiveness of interventions that help cattle to maintain thermal homeostasis (homeothermy). Differences in the thermal physiology of *Bos taurus* and *Bos indicus* subspecies of cattle will specifically be examined.

Thermodynamics

Thermodynamics is the branch of physics that deals with heat, work, and temperature. The primary unit of thermodynamics is the watt (W) which is the rate of transfer of energy (i.e. work). One watt is equal to 1 J/s of energy (e.g. heat) transfer. Thermodynamics has four axioms:

1. Systems are in thermal equilibrium when there is no net exchange of energy between them.
2. Energy within a system may be transformed or transferred between systems as heat and/or work, but energy cannot be created or destroyed.
3. Energy (heat) cannot flow spontaneously from locations of lower energy to locations of higher energy. Entropy is a measure of the disorder of a system, with energy only able to move spontaneously from a more ordered to a less ordered state (e.g. solid to a liquid).
4. The energy and entropy of a system approaches a minimum as the temperature of the system approaches absolute zero (0°K; −273.15°C). Warmer molecules are more energetic molecules. The energy of a molecule is expressed in its movement via $KE = ½mv^2$ (where KE is kinetic energy, m is mass, and v is velocity). Since m is a constant for a given molecule, more energy equals more velocity.

The total energy of a system (such as the body of an animal) is contained within the kinetic and chemical characteristics of its constituents. Energy can transfer into a system through heating, compression, or the addition of matter. The removal of heat from a system is the removal of energy and produces a change in either or all of temperature, compression (pressure), phase of components (e.g. liquid versus gas), or the amount of matter in the system. While the body of an animal can be considered as a system, it is not hermetically sealed, and so exchanges energy with the environment. That is, the system is open.

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Heat exchange between the body of an animal and its environment occurs from the combination of radiation, convection, conduction, and evaporation. Radiation is the transmission of energy as electromagnetic waves. Convection is the transfer of heat due to the bulk movement of molecules within fluids (liquids and gases, not solids). The convective movement of molecules proceeds away from a source of heat by random Brownian motion (called free convection) and by advection (large-scale currents, called forced convection). Heat exchange by convection depends on the temperature of the animal surface, the temperature of the fluid in contact with the animal surface, the surface area of contact, and the wind speed. Conduction is the movement of energy through a continuous substance (from hot to cold) and arises from collisions and the transfer of energy from more energetic to less energetic molecules. Conduction occurs in solids, liquids, and gases. Evaporation is the vaporisation of molecules from the surface of a liquid as molecules change from the liquid to the gas phase. The phase change requires energy, which is derived from the evaporating surface, thus cooling it.

Radiation, convection, and conduction involve the transfer of "sensible" heat between objects and results in a change in the temperature of both objects. Evaporation transfers "latent" heat and this does not change the temperature of both objects. In the transfer of latent heat from a liquid on the surface of an animal to the surrounding air, energy (and heat) is lost from the liquid, which is in contact with the body surface, but the temperature of the air does not change. Instead, the energy is manifested as an increase in the water vapour pressure in the air. Sensible heat transfer can occur in both directions (from the animal to the environment or from the environment to the animal). Latent heat transfer is nearly always from the animal to the environment (air), although in very rare instances condensation can occur on an animal surface, in which case latent heat is added to the animal. The magnitude of sensible heat transfer depends primarily on the temperature gradient between the two objects and the surface area of contact, whereas latent heat transfer is determined primarily by the degree of wetting of surfaces, their area, and the water vapour pressure of the air.

Animals physiologically manipulate the level of heat exchange by each of these routes in a way that balances heat gain with heat loss. When they are in balance, the heat content, and therefore the temperature, of the body is stable. When there is an imbalance, body temperature will rise or fall, resulting, respectively, in hyper- or hypo-thermia. The various avenues of heat transfer between mammals and their environment are summarised in a recent review by Mitchell et al.[3]

Animal responses to stress

Homeothermy is the maintenance of a relatively stable internal body temperature regardless of external conditions.[4] Cattle are homeotherms and exposure to very hot or cold environments can challenge their homeothermy, thereby inducing thermal stress. An animal's responses to stress can include behavioural, metabolic, and physiological changes.[5] The response to thermal stress is somewhat arbitrarily divided into acute and chronic responses. Acute responses to thermal stress occur within minutes to a few days following exposure to thermal stress and are driven primarily by the autonomic nervous system, which controls part of the endocrine system (leading primarily to the secretion of catecholamines and glucocorticoids) that produces changes in behaviour and metabolism. Acute homeostatic responses are reflex responses that quickly restore bodily processes to normal functioning. Chronic responses to thermal stress are observed after a few weeks to months of continuous exposure to a stressor, and are mostly driven by the endocrine system, which alters cellular activity and "resets" the physiology of the animal to a state that makes the animal more able to manage the persisting stress. The process of this response is termed acclimatisation if the stressor is natural, such as a change in season, or acclimation if the stressor is experimentally applied. Both processes result in physiological and/or behavioural changes within the lifetime of an organism that reduce the strain caused by a given stressor.[4] Chronic adaptation to thermal stress involves changes to energy and protein metabolism, water balance, acid–base balance, and endocrine status. Importantly, acclimatisation to heat stress leads to an enhanced capacity of an animal to dissipate heat. The outcome of the changes in physiology can lead to a reduction in productive and reproductive performance.[6] The responses of individual animals to the same stress can differ, despite identical environmental conditions.[7]

Changes that occur with acclimation/acclimatisation can include altered morphology, behaviour, physical traits, and/or biochemistry. The acclimatisation of cattle to heat takes between 2 and 7 weeks.[8] The acclimatisation of cattle to cold has been reported to take several weeks.[9] Heat acclimatisation includes the combined effects of a reduction in metabolic rate (by up to 25%, which reduces the generation of metabolic heat), expansion of the vascular space (which increases the capacity to transfer metabolic heat to the skin for convective, conductive, and radiant heat loss from the surface of the body), enhanced capacity for evaporative cooling, and changes to surface insulation (coat change).[3] When they are exposed to a heat wave, cattle that have been acclimated to heat exhibit smaller increases in rectal temperature than do unacclimated cattle.[10]

Heat stress is an important welfare consideration. Public attitudes to the management of dairy cows show a strong preference for cows to be kept outdoors (on pasture, as opposed to housed) and for the provision of shade.[11] Importantly, when asked to choose between open grazing or access to shade to prevent heat stress (i.e. housing), the public had a strong preference for the minimisation of heat stress over access to pasture. Open-ended questions indicated that most respondents viewed a failure to provide adequate shade as a failure of the farmer's duty of care towards their cows.

Responses to heat stress

Heat (thermal) stress occurs whenever a homeothermic animal is required to increase evaporative heat loss to maintain heat balance, and a constant body core temperature. The ambient temperature above which a homeotherm must increase evaporative heat loss to maintain heat balance is called the upper critical temperature (UCT). During exposure to mild heat stress, just above the UCT, cattle will adjust heat transfer by modifying radiative, conductive, convective, and evaporative heat exchange. They do that primarily by increasing the flow of blood to the skin, which increases the delivery of metabolic heat that is produced by internal organs to the periphery from where it is lost to the environment by convection, radiation, and the evaporation of sweat from the skin or fluid from the upper respiratory tract. When environmental temperature exceeds the temperature of the skin surface (at around 36°C), heat will flow from the warmer air to the cooler skin, and thus add heat to the body. At that stage, to maintain thermal balance, evaporative cooling must increase to match the extra heat load because those cattle are now completely reliant on evaporative cooling to dissipate heat. Similarly, exposure to solar radiation leads to radiant heat gain and helps to explain why shade can improve the welfare of cattle even though the air temperature under shade is the same as outside of it.

The effects of exposure to heat stress can range from minimal through mild discomfort to suffering, extending finally to death. When they are exposed to heat stress, cattle reduce feed intake which reduces their metabolic rate and so decreases the metabolic heat load on the animal. The suppression of appetite in heat-exposed cows has been observed to persist for several days after a return to benign conditions, which is thought to reflect the time required for hormone-induced changes to revert to normal. Some chronic responses (e.g. changing coat thickness) occur over weeks. Exposure to heat stress activates genes including heat shock proteins and heat shock transcription factors and these variable impact on the endocrine and immune system.[12] Most endocrine responses occur via the hypothalmic-pituitary–adrenal axis, resulting in elevated circulating corticosteroids, which inhibit the production of inflammatory mediators and result in a reduction in immune function.[13] An increase in the levels of these hormones can be used as an indication of heat stress, but the most used physiological indicators of heat stress in cattle are elevations in rectal temperature, respiratory rate, drooling, sweating, and a reduction in dry matter intake and behavioural indicators such as reduced time spent lying (with a concomitant increase in time standing) and reduced time spent feeding.[14] Other negative impacts such as decreases in production (growth, milk, etc.), feed intake and appetite and increases in respiratory rate, panting, drooling, core temperature, heart rate and sweating as well as reduced reproductive performance, lying, walking, and increased aggression and dominance behaviour (especially related to shade seeking) are non-specific indicators that may occur during heat stress.[6]

Responses to cold stress

Cattle respond to cold exposure by decreasing the perfusion of the skin (vasoconstriction) that in turn decreases the delivery of metabolic heat from internal organs to the skin, leading to a reduction in skin temperature and therefore less heat loss by conduction, convection, radiation, and evaporation. When the reduction in heat exchange by those routes is insufficient to limit heat loss to the same level as heat gain (which is primarily metabolic heat production), then the animal must increase metabolic heat production via either shivering or non-shivering thermogenesis. The temperature below which a homeotherm must increase metabolic heat production is called the lower critical temperature (LCT). The LCT for dairy cattle is about −5°C for calves, −14°C for adults and dry cattle, and −25°C for lactating cows.[15]

Vasoconstriction increases the insulation of the animal because non-perfused tissues in the periphery act as a barrier to heat loss. The insulation is increased further by piloerection, the erection or bristling of hairs due to the reflex contraction of muscles at the base of hair follicles. Piloerection can double the depth of the coat and increase coat insulation, thereby reducing heat loss by radiation, convection, and conduction. Piloerection is more effective in cattle with winter coats.[16] When an increase in metabolic heat production is required to maintain heat balance, cattle will shiver. Shivering is the involuntary, rhythmic contraction of skeletal muscle that results in no functional movement or work output.[17] During shivering, antagonistic muscles are activated simultaneously, whereas during normal motor control, the activation of a muscle usually is accompanied by inhibition of the antagonistic muscle. Shivering is very energy-demanding and cannot be sustained for long periods. Newborn cattle are especially prone to cold stress because of their high surface area/mass ratio and they are poorly insulated at birth (coat and subcutaneous fat).[16] Newborn calves are also monogastric and so do not obtain any heat from rumen fermentation. Calves are capable of non-shivering thermogenesis, which involves the activation of brown adipose tissue (BAT), a specialised fat tissue that is well-perfused.[18] The mitochondria in BAT express uncoupling protein on the inner mitochondrial membrane, which uncouples oxidation from phosphorylation, and the chemical energy that is usually captured in the terminal bond of ATP is instead dissipated as heat. Whether physiologically-relevant depots of BAT persist in adult cattle is presently unknown. Twenty years ago, it was thought that BAT atrophied after infancy in mammals that do not enter torpor or hibernation, but there is no evidence of functional BAT in many adult mammals.[19]

Pathologies that are observed in severe cold exposures include subcutaneous oedema and haemorrhage, intra-articular haemorrhage, synovitis in the limbs, and elevated serum total protein, red blood cell counts and packed cell volumes.[16] Cold exposure increases the demand for energy via an increase in the metabolic rate, resulting in increased appetite, feed intake, and energy expenditure. When they were moved from a 10°C to a −15°C environment, dairy cows showed an increase in plasma thyroxine levels that were associated with a 35% increase in metabolic activity and heat production.[5] Lower-producing dairy cows have a lower metabolic rate and heat production than high-producing dairy cows,[20] and thus high-producing can better tolerate lower temperatures.[21,22]

Thermoregulation

Thermoregulation is the process of maintaining core body temperature within a narrow range (i.e. homeothermy). Homeothermy is thought to optimise organ and system function. Homeotherms control heat exchange between their body and the surrounding environment so that heat loss and gain are in balance, and so body heat content and therefore body temperature remains stable. They can achieve heat balance across a wide range of environmental conditions, called the prescriptive zone.

Thermal homeostasis can be described as[7]: $HG - HL = \triangle Tbody \times cp \times m$, where, HG = heat gain (from metabolism, activity and environment), HL = heat loss (to the environment), $\triangle$Tbody is the change in body temperature, cp is the specific heat of the body (3.47 kJ kg^{-1}°K^{-1}), and m is the body mass (kg). The relationships between heat gain and loss can also be expressed as a heat balance equation: $HS = M \pm HCD \pm HCV \pm HRAD - HER - HES$, with each term expressed in watts where HS is the net heat stored in the body, M is the metabolic heat production, HCD is the exchange of heat by conduction, HCV is the exchange of heat by convection, HRAD is the exchange of heat by radiation, HER is the heat loss by evaporation in the respiratory tract, and HES is heat loss by evaporation due to sweating.[23] The Brown-Brandl equation states that the accumulation (or loss) of heat energy by the body presents as a sustained change in body temperature.[7] It should be noted that transient changes in body temperature are tolerated and somewhat normal in free-living animals.[3] A persistent change in body temperature occurs when heat exchange mechanisms are overwhelmed.

The relationship between body core temperature and the ambient temperature can be described using several zones that demarcate different physiological responses to the environmental stimulus.[3] The narrowest, and central, zone is the thermoneutral zone (TNZ), defined as that range of ambient temperatures where temperature regulation is achieved using only adjustments to sensible heat loss mechanisms, and with no change in metabolic heat production. The TNZ is bound between the air temperature at which the metabolic rate must increase (the LCT) and the air temperature when evaporative cooling mechanisms must be initiated (UCT) to maintain homeothermy. By definition, the exposure to conditions outside of the TNZ is thermal stress; the definition given by the IUPS Thermal Commission (2003) is "any change in the thermal relation between a temperature regulator and its environment which, if uncompensated by temperature regulation, would result in hyper- or hypothermia".[4] Thus, by definition, a homeotherm is under thermal stress whenever it is outside of its TNZ.

On either side of the TNZ is the prescriptive zone (PZ) that defines the range in ambient temperatures where heat balance can be achieved, and so body temperature is held constant; but metabolic rate or evaporative heat loss will increase to achieve balance. In this range, metabolic rate increases at low temperatures and evaporative cooling increases at high temperatures, meaning that more energy or more water is required for homeothermy. Expanding beyond the PZ is the tolerance zone (TZ). At these extremes, homeothermy is no longer maintainable despite increased metabolic or evaporative activity, however, the animal's life is not immediately threatened as the change in body temperature is minor. Exposure within the TZ does present a long-term risk to organ functioning and species survival at a population level (e.g. due to declining reproductive performance). The widest range is the survival zone (SZ) within which the survival of individuals is not at risk, but beyond those limits, individuals will die within hours to days.

Most free-living animals voluntarily spend time outside of their prescriptive zone (but within the limits of the tolerance zone). They can survive long periods (or indefinitely) with regular forays to the extremes of the tolerance zone and so some regard the limits of the tolerance zone to define the safe welfare limits for animals.[3] This may have importance for interpreting when thermal stress becomes a welfare concern. The presence of any physiological and/or behavioural responses to altered thermal exposure does not always indicate adverse welfare; animals periodically venture into extreme environments for personal advantage (e.g. to find food, and mates) and it is this capacity that has contributed to the ecological success of homeotherms.

The definitions given above are classified by air temperature. But heat exchange depends on other factors aside from air temperature, and so changes in those other factors modify the limits of the various zones. For example, exposure to solar radiation increases radiative heat gain and moves all the zones to the left, an increase in wind speed increases convective heat exchange and moves all the zones to the right, and an increase in humidity reduces evaporative heat exchange and will move all the limits above the TNZ to the left. Thus, unless they are housed in air-conditioned enclosures, like some thoroughbred racehorses, most production animals will spend little of their lives within their TNZ. But it is unlikely that most people would classify those animals as always thermally stressed. When it is in full fleece, a sheep may pant at an ambient temperature of 22°C[24] but it is unlikely that anyone would consider exposure to 22°C a welfare issue for sheep.

Heat sources and sinks

Heat is generated internally from digestion, basal metabolism, activity, and production. External heat can transfer into the body via radiation, conduction, or convection. Body heat can also transfer to the environment by these means, and by evaporation. The digestion of food releases heat, especially fermentation in the rumen; because of that local heat source, rumen temperature is generally about 1°C higher than the core temperature in cattle,[25] and about 0.5°C higher than the core temperature in sheep.[26] The rumen temperature of cattle eating *ad libitum* was higher, and had a different diurnal pattern, than the temperature in cattle held to a limited intake.[27] Basal metabolic heat derives from the maintenance of basic cell function, especially the pumping of ions to maintain the resting cell voltage, heat from muscle activity, and the production heat from other physiological processes that produce growth, lactation, pregnancy, and anything that involves protein or fat production or deposition.

When an animal is at rest, metabolic heat is produced mainly in the organs of the "core", including the heart, liver, kidneys, brain, and gastrointestinal tract. The heat must be transferred from the body core to a body surface that is in contact with the environment. The transfer requires a temperature gradient between the body core and the surface, and while some heat flows by conduction from the warmer organs to the skin, most are carried in the blood. The transfer of heat from a body surface to the environment also requires a temperature gradient for conduction, convection, and radiation, and a water vapour pressure gradient for evaporation. Heat will flow from the animal to the environment whenever the skin is warmer than the surrounding air (by convection), whenever the skin is warmer than anything that the skin can "see" (by radiation), or whenever the skin or surfaces of the upper respiratory tract are at a higher water vapor pressure than the surrounding air. Because the skin temperature of cattle is around 36°C, heat will move from the animal to the environment whenever that environment is below 36°C.

When the ambient temperature decreases toward the LCT, as defined earlier, the transfer of heat from the core organs to the skin is reduced, that is, the periphery will become vasoconstricted. That vasoconstriction holds heat within the core and facilitates the maintenance of core body temperature. When vasoconstriction is maximal and heat loss still exceeds metabolic heat production, then the animal must increase the production of metabolic heat by shivering or non-shivering thermogenesis. The point where metabolic heat production increases is the LCT, as defined earlier.

Because the exchange of heat between the body and the environment occurs across a body surface interface, the exchange is proportional to the surface area. Larger animals have a lower surface area to body mass ratio than smaller animals. Thus cattle, like other large mammal species, have a lower surface area to volume (weight) ratio and so lose proportionately less metabolic heat from their surface than smaller species under similar conditions.[3] This is also the case for larger cattle compared to smaller cattle. Consequently, the LCT of smaller cattle will be higher than it is for larger cattle. The same principle applies to the UCT, as we will discuss subsequently.

Metabolism. The rate of metabolic heat production is a major component of the heat balance equation, and so is an important determinant of the LCT and the UCT. An estimate of maintenance energy requirement for cattle is as follows: MJ $day^{-1} = 0.34 \times$ (body mass [kg])$^{0.75}$.[28] *Bos taurus* typically have a metabolic rate that is 15%–20% higher than *Bos indicus*. The metabolic rate varies between breeds, and for cattle of different body conditions and acclimatisation histories; the difference can be 25% between breeds and 33% between individuals of the same breed.[29] Dairy breeds have higher metabolic rates than beef breeds, and for dairy cattle, the rate varies with an individual's milk production; high-producing individuals have a higher metabolic rate than low-producing individuals.[5,22] A Holstein in good (fat) body condition originating from a cool environment (acclimated to 10°C daily maximum) will have an average basal metabolic rate of around 47 MJ d^{-1} while a lean Brahman from a tropical environment (acclimated to a 30°C daily maximum) will have a rate of around 24 MJ d^{-1}. Breed, body condition, and acclimatisation are risk factors for thermal stress that can be manipulated by management.

High feed intakes promote an increase in metabolic rate. Homeotherms often respond to heat exposure by reducing feed intake, which is often interpreted as an adaptive response that slows the metabolic rate and therefore the generation of metabolic heat. A reduction in feed intake occurs at lower temperatures in *Bos taurus* cattle than it does in *Bos indicus* under heat exposure.[30] Conversely, cattle exposed to cold will increase their metabolic rate thereby increasing the generation of metabolic heat and subsequently their appetite.[16] Diet composition can also affect metabolic heat generation. Between 35% and 70% of metabolisable dietary energy can result in the generation of heat (non-usable for work). Fibre is especially associated with the generation of non-work-usable heat. Reducing the fibre content of a diet can reduce heat production.

Activity. Dairy cows use around 55 J $kg^{0.75}$ m^{-1} when they walk, equating to about 7 MJ net energy for a 600 kg cow to walk 1 km. Most of the energy that is metabolised for maintenance and activity is eventually converted into heat,[31] meaning that physical activity can impact heat balance and ultimately welfare. Cattle exposed to hot conditions will spend less time walking, more time standing, and less time lying.[32] It might seem counter-intuitive that cattle would stand more in the heat, given that standing has a higher metabolic cost than lying. But a lying cow has less of its surface area exposed to the surrounding air, and so, on balance, it is thought that standing improves heat exchange by convection and radiation during heat exposure.

Standing cattle were observed with core body temperatures that were 0.7°C higher than those of lying cattle, suggesting that an increase in core temperature stimulated the shift from lying to standing. Supporting that argument, cows that switched from lying to standing had higher core temperatures than cows that were continually lying or standing.[33] Cows with higher core body temperatures stood for longer than cows with lower core body temperatures and core body temperature could predict when cows initiated the change from lying to standing.[34] Standing when it is hot increases the exposure of the skin surface and so facilitates evaporative, convective, and radiant heat transfer, and reduces the generation of heat from activity.[33] Conversely, cold-exposed cattle lie more. The proportion of animals in a pen that is lying or standing (and the duration of standing) can provide insight into how animals are coping with the thermal conditions.

Radiation. Radiant energy is electromagnetic energy that is transmitted in waveform. Everything that is warmer than absolute zero emits radiation, with the intensity of that radiation increasing with temperature, while the wavelength that is emitted decreases with temperature. At biological temperatures, radiation is emitted in the infrared. More than half of incident solar radiant energy, and all of the radiation emitted from an animal's surface, is infrared.[3] The former is "near" infrared while the latter is longer wavelength "far" infrared. This means that light pathways and light intensity are not always effective indicators of total radiant heat exposure. While lighter-coloured coats absorb less visible radiation than darker coats, the infrared emissivity (and thus heat loss) is independent of coat colour.

The net exchange of heat by radiation depends on difference between the 4th power of the temperature of the animal surface, the total surface area, and the 4th power of everything that the animal's surface can "see" ("see" is in inverted commas because most of the radiation is outside of the visible spectrum). The latter temperature is the radiation temperature of the environment. Indoors, the radiation temperature can be close to the air temperature, but outdoors the two are generally quite different. This means heat exchange by radiation is not related to the air temperature.

The exchange of radiant energy in cattle is influenced mostly by latitude, season, environmental conditions, orientation of the animal to the sun and the reflective and absorptive characteristics of the coat. The radiant heat load that is incident on sun-exposed, grazing, dairy cows is around three times their rate of metabolic heat production.[35] Most cattle in Australia are exposed to at least 150–300 W m^{-2} of radiant heat energy, but the load can exceed to 1 kW m^{-2} in the hottest part of the day in northern regions of Australia.[3] In tropical regions, the peak rate of absorption of radiant heat in grazing Holstein cows was estimated at 640 W m^{-2}.[36] A 500 kg, acclimated, moderate body condition Angus cow with 2 m^2 of skin exposed to direct sunlight has a metabolic rate of around 40 MJ d^{-1}, equating to a rate of metabolic heat production of 350 W. At a latitude of 20°, and in full sun exposure the animal would absorb an average of 285 W m^{-2}, equating to 570 W for the animal. That is more than 1.5 times the rate of metabolic heat production. It is clear from this example that the radiant heat load can be the largest single component of the heat balance of cattle in some circumstances.[37] The protection of vulnerable stock from radiant heat by providing adequate shade is thus essential to prevent heat stress.

While radiant heat input can be the dominant term in the heat balance equation, loss of heat by radiation can also be quantitatively important. In tropically-adapted Nelore cattle, 60% of the daily metabolic heat production was dissipated by radiation.[38] Cattle can readily dissipate heat by radiation and convection when they are not exposed to direct sunlight and at moderate ambient temperatures. The radiation temperature of the clear night sky is sub-zero, and cattle exposed to a clear cool night sky can radiate significant heat to the atmosphere.[3] This can help with the heat balance of animals exposed to heat stress risk during the day but can be a risk for cold stress in animals exposed to severe cold.

A lactating dairy cow with a skin temperature of 36°C will radiate around 500 W m^{-2}, equating to 3.27 kW for a 600 kg cow, which is about one-third of their metabolic heat production.[39] Because radiant exchange occurs between any two surfaces that "see" each other, heat is transferred between animals by radiation. Thus, stock density impacts the distance between animals and subsequently the rate of between-animal radiant heat transfer. Changing stock density can modify this heat stress risk. The provision of shelter, insulation (bedding), and the management of stock density are important ways to minimise radiant heat loss in cold-exposed cattle.

Convection. Convection is the transfer of heat due to the bulk movement of molecules within fluids. For cattle, this predominately involves the heating (and removal) of the air around the body. Because the density of air is inversely related to its temperature, hot air is less dense than cooler air, and thus hot air rises. When heat flows from an animal surface to the air surrounding it, that air warms and becomes less dense, creating a natural current of air movement around the animal. That exchange is called "free" convection. When the air surrounding an animal is moved by external forces, like weather patterns that generate wind, that is referred to as "forced" convection. The exchange of heat by convection is proportional to the square root of the wind speed.

The exchange of heat by convection also depends on the surface area that is exposed to convection, and the shape of the exchanging surface, as defined by its Reynold's number. Narrow and long surfaces have a higher Reynold's number than short and wide surfaces, and all else being equal will have higher convective heat exchange. Animals with long, narrow limbs and appendages (dolichomorphic shape) lose more heat by forced convection than barrel-shaped, short-limbed species.[3] Because convective heat exchange is affected by wind speed, shelters can provide protection against convective loss to the sky (roof) and from wind convection (walls).

Conduction. Conduction is the transfer of heat through the contact of an animal surface with another (mostly solid) substance. The exchange of heat by conduction depends on the temperature difference between the two substances that are in contact, the area of contact, and the thermal conductivity of the two substances. Conduction is generally a minor component of heat exchange when an animal is standing but can be substantial if an animal lays on the ground. For cattle, conduction occurs primarily with the ground. Because the rate of heat transfer by conduction depends on the area of contact the rate of conduction of heat into cooler ground is higher when cattle are lying compared to standing. Lying cattle tend to have a lower rectal temperature but a higher cutaneous temperature than standing cattle.[40]

Because the thermal conductivity of water is much higher than the thermal conductivity of air, the thermal conductivity of a cattle coat increases when it is wet. Cattle will reduce lying time when they are cold and wet. The insulation characteristics of bedding/flooring and the quality of bedding, especially its dryness, are important considerations in the management of conductive heat exchange. For example, sand has a higher thermal conductivity than wood, and so heat-exposed dairy cows can dissipate more to sand bedding than to sawdust bedding.[41]

Evaporation. Evaporation occurs when molecules near the surface of a liquid transition to the gas phase. A molecule requires a threshold kinetic energy to overcome the inter-molecular forces within a liquid and enter the gas phase. Because only the most energetic molecules in a liquid make the transition to the gas phase, the molecules that remain in the liquid phase are less energetic, and so are at a lower temperature. The rate of evaporation is determined by the surface area and temperature of the liquid, air pressure, and the water vapour pressure of the atmosphere in contact with the liquid (vapour pressure). The amount of energy that is required depends on the temperature of the liquid but ranges between 2.26 and 2.50 kJ g^{-1} for water between 1 and 99°C (e.g. 2.44 kJ g^{-1} at 25°C). Thus, at the normal surface temperature of an animal, 2.44 kJ is removed from the surface when 1 g of sweat evaporates from the skin or 1 g of water evaporates from the respiratory surfaces.[6]

Evaporative mechanisms are vitally important because when the ambient temperature approaches (or exceeds) body temperature, the temperature gradient that drives heat exchange by radiation, conduction, and convection is decreased, lost, or reversed. Cattle thus become increasingly reliant on evaporative mechanisms as ambient temperature increases.[8] Because the rate of evaporation to air depends on the area of the wet surface, larger animals can dissipate more heat (absolutely) than smaller animals. But because smaller bodies have a larger Reynold's number than larger bodies, when wind speed increases, small animals will lose relatively more heat by evaporation than will larger animal.

In cattle, evaporative cooling occurs via sweating and panting. Although cattle can pant, most of their latent heat loss is by sweating (75%).[7] The effectiveness of evaporative cooling is influenced by humidity, wind speed, respiratory rate and volume, and the density and activity of sweat glands. Panting and sweating are energetically efficient; there is no increase in the metabolic rate when cattle begin to sweat or pant.[3] Animals that can meet their demand for water and electrolytes can maintain high rates of evaporative cooling for prolonged periods.[3] This implies that simply observing strong evaporative cooling activity in cattle is not necessarily an indication of a failure to cope; the duration and quality of recovery might be more pertinent.

Evaporative cooling via panting. Because respiratory surfaces are always wet, evaporation occurs from the respiratory tract, even in cold conditions, every time an animal breathes. Panting amplifies the process by moving more air over those wet respiratory surfaces. Panting is stimulated by an increase in the firing rate of either core or peripheral warm-sensitive thermosensors. Because peripheral thermosensors can stimulate the panting response, cattle can pant in hot conditions before core temperature increases,[42] although there are reports of a lag in the panting response by cattle when they were exposed to an increasing air temperature in a climate chamber.[43] Conversely, when effective external cooling by skin wetting is applied to hyperthermic cattle; their respiratory rate decreases immediately, before core temperature had time to change.[44]

While panting is often triggered by an increase in core or peripheral temperature, there are other non-heat-related causes of panting in cattle such as respiratory compromise, disease (such as pneumonia), or circulatory failure.[45] While respiratory rate and panting are sensitive indicators of heat stress in cattle, they are not specific. The proportion of cows in a group that is breathing heavily can be more useful than monitoring the panting of individuals because of the variability between individuals. When the vaginal temperature and panting frequency of individuals were monitored as they were exposed to heat, only about 10% more animals breathed heavily for every 0.5°C rise in vaginal temperature above 39.0°C.[42] Thus, some individuals were panting with a vaginal temperature of 39.1°C but others did not pant even with vaginal temperature of 41°C.

Cattle have a biphasic respiratory response to heat exposure that is characterised by the panting response; shallow, rapid breathing in the first phase of exposure to heat load, moving to a slower and deeper (higher tidal volume) breathing in the second phase.[46,47] The stimulus for the change in breathing pattern is likely to be further elevation of body temperature. While Phase I panting involves an increase in minute ventilation, the increase is largely restricted to the dead space of the respiratory tract and there is no change in alveolar ventilation. The change to Phase II panting leads to an increase in alveolar ventilation, with consequent impacts on carbon dioxide excretion and acid/base balance, leading to hypocapnia and respiratory alkalosis. When a run of hot days occurs, cattle that enter the next (hot) day with an elevated pant score are likely carrying excessive heat load from the previous day (i.e. they have an elevated morning body temperature) and are at increased risk of compromise due to heat exposure.[48] Scoring systems for panting frequency and quality have been developed to explore the relationship between panting score and temperature.[48]

Evaporative cooling via sweating. Sweating is the main avenue for evaporative cooling in cattle. Sweat glands are present throughout the skin of cattle and those glands are under central control. *Bos indicus* cattle have a higher density of sweat glands and the glands are larger, resulting in a purportedly higher sweating rate, than *Bos taurus*.[8] However, evidence for breed differences in sweating rate is not strong. A study found maximal sweating rates of around 500 g m^{-2} h^{-1} for Holsteins and 650 g m^{-2} h^{-1} for *Bos indicus*.[22] Another study observed a maximal rate of water loss due to evaporative cooling in 600 kg lactating dairy cows of 1.5 kg h^{-1}.[6] Using an estimate of surface area for such a cow of 6.54 m^2, that value of 1.5 kg h^{-1} implies maximal sweating at only 230 ml m^{-2} h^{-1}, which is quite a bit lower than that reported by Berman.[39] When *Bos indicus* and *Bos taurus* heifers of similar body mass (335 kg) were placed into a climate chamber and exposed to the same, gradually rising, ambient temperature and humidity, the core temperature of the *Bos indicus* did not increase significantly until the wet-bulb temperature[i] exceeded 30°C, while the core temperature of the *Bos taurus* increased 4 days earlier, when the wet-bulb temperature was 26°C.[30] It is not known whether the better capacity to achieve heat balance in the *Bos indicus* was because of a higher capacity for evaporative heat loss, or because of a lower metabolic heat load, or a combination of the two. In those same experiments, the *Bos taurus* heifers increased their respiratory frequency when the wet-bulb temperature was 26°C, while *Bos indicus* increased only when the wet-bulb reached 28°C. When the respiratory frequency did increase, the respiratory frequency of the *Bos indicus* remained lower than that of the *Bos taurus* until the wet-bulb temperature has been at 32°C for 5 days.[30]

Sweating cattle will maintain a constant skin temperature of about 36°C irrespective of the air temperature. This is a thermodynamic feature of wet surfaces that are undergoing evaporative cooling.[3] The provision of sufficient drinking water and the replacement electrolytes is critical to enable effective sweating and panting by cattle, while ventilation of the air surrounding the cattle (with air that is at a lower water vapour pressure) will enhance the cooling effect by enhancing evaporation from the cattle. Assuming a lower maximum evaporative cooling from cattle of 500 g m^{-2} h^{-1}[49] at a wind speed of 1.0 m s^{-1} results in evaporation of 3.3 l h^{-1} for a 600 kg Holstein, which would remove around 8 MJ h^{-1}. Thus, the maximum capacity of the evaporative system can remove heat at 3–4 times the rate of maintenance heat production.

Measuring thermal balance

Short of the continuous measurement of core body temperature in every animal that is exposed to heat stress, it remains challenging to identify when cattle begin to lose their ability to maintain heat balance and homeothermy, or other aspects of homeostasis that are impacted by the response to heat exposure, such as the development of respiratory alkalosis. Early responses to failing homeothermy are not clear; there is no recognised demarcation point between coping and failing homeothermy. This is partly because of the interplay between the magnitude and duration of heat exposure, the susceptibility of individual animals and the environment, and animal

[i] The wet bulb temperature is the temperature recorded by a thermometer covered in a water-soaked cloth. It measures the temperature of a parcel of air cooled to saturation. The wet bulb temperature provides insight into the effectiveness of evaporative cooling.

management. The main measurements that have been used to assess the issue are discussed below.

Body temperature

The body temperature of each species of homeotherm varies within a defined range, and individuals within a species can differ. Body temperature has a natural daily rhythm, oscillating by less than 1°C each day.[50–52] The diurnal range of body temperatures in healthy cattle in summer is larger than it is in winter, suggesting that the circadian rhythm of body temperature changes due to the duration and magnitude of changing heat/cold exposure and/or day length.[53] The mean daily body temperature can vary between and within individuals over time. This makes it difficult to define a range of normal body temperature in homeotherms. The body temperature of an individual animal may be within 'normal' range for some combinations of species, age, physiological status and acclimatisation but the same temperature may indicate failure of homeothermy on other occasions. There are reports of a diphasic daily rhythm in cattle,[40,54] and monophasic or polyphasic rhythms.[54] Part of the variation between studies is probably due to differences in ultradian rhythms (more correctly called episodic ultradian events) between the cattle in the different studies.[55]

Body temperature can vary between body sites and with age, and changes in known ways with physiological status and stage of the reproductive cycle.[56,57] The temperature at different body sites also tends to differ in magnitude and cyclicity; any temperature that is measured near the periphery of the body will display a larger daily amplitude than will the true core temperature. Rumen temperatures peak mostly at night, whereas rectal temperatures peak mostly in the afternoon.[58] Rumen temperatures were also observed to be higher than rectal temperatures.[59] Subcutaneous temperatures tend to be lowest in early morning and peak around midnight in normal cattle and are up to 2°C lower than rectal temperatures at the same times of day.[60] In one study on housed cattle, their vaginal, rectal, and reticular temperatures of the cows were only moderately correlated.[61] Another study on cold-exposed cattle found (paradoxically) that vaginal temperatures increased in cattle exposed to cold compared to cattle exposed to normal or hot conditions.[62] Cattle exposed to 16 h of −15°C temperatures per day had elevated vaginal temperature compared to cattle exposed to up to 22°C over a similar period. Researchers have concluded that these changes arise primarily because of changes to circulation (i.e. due to vasomotor control), and not due to changes in metabolic heat production.[62] The body temperature and ambient temperature diurnal cycles appear to be statistically linked,[63] but that may simply be that the natural cycle of the two variables is in phase (i.e. the body temperature relationship to ambient temperature shows hysteresis). This presents as a lag in the elevation of body temperature (beyond a threshold) compared to the elevation of ambient temperature (beyond a threshold). The timing and magnitude of the daily peak of body temperature in cattle varies by season. Peak body temperatures were observed to be lower and to occur earlier in the day in winter than in summer in dairy cattle.[57] Numerous authors have concluded that to allow for comparability between studies, continuous and standardised body temperature monitoring is required in studies that explore the effect of heat- or cold-exposure.[64] Single one-off measurements, or daily temperature recordings based on a few measurements per day are likely insufficient for assessing homeothermy except in the extremes. Body temperature lags an average of 4 h after an increase in ambient temperature in animals exposed to acute heat stress, and by an average of 3 h for animals exposed to chronic heat stress.

There is quite a wide variation in the "normal range" of body temperature that has been reported for cattle, including (rectal) 38–39°C,[65] (reticulum) 34.4–39.2°C[40] and (rectal) 38.6–39.2°C, with a daily mean of 38.3°C[56] have been variously reported. The reported threshold for fever in cattle ranges from (rectal) 39.4–39.7°C.[66] There are reports that after calving, cows that appear otherwise healthy can exhibit periods of 'fever' for many days, further suggesting that the upper range of temperatures is not clearly defined.[66] The proportion of housed (i.e. not exposed to direct sunlight) and clinically normal cows with body temperatures above a chosen threshold of 39.5°C was 7.4% under moderate heat (temperature humidity index of 59.8 ± 3.8), increasing to 28.1% under a hot (temperature humidity index of 74.1 ± 4.4) environment.[65] The development of automated systems for detecting fever events in cattle has been challenged by this natural variation.[60]

The maximum body temperature for a day was found to be positively correlated with the minimum body temperature (typically the night-time minimum) of the preceding day.[67] This suggests that animals that fail to restore body temperature during the cooler time of the day are at greater risk of heat stress the following day under similar heat exposures. The minimum, and not the maximum, body temperature is potentially more useful for monitoring homeothermy under heat exposure, and vice-versa for cold exposure. Alternatively, the daily maximum and minimum core body temperatures, and thereby the range, may be a more useful way to assess homeothermy than the comparison of a single value against a defined distribution.[52] The search for non-invasive ways to measure thermal stress, including studies of changes to the behaviour, physiology, emissivity and the faecal microbiome are being explored,[68] perhaps culminating in artificial intelligence assessments of multiple variables.

Environmental conditions

Environmental temperature is the primary parameter that has been used to define the risk of heat stress. Other parameters that influence total heat load include solar radiation, humidity, and wind speed, which affect radiative heat transfer and evaporative cooling efficiency and are therefore important considerations in assessing the risk of compromise under conditions of heat stress. Various indices have been developed in attempts to capture the influence of all the variables that impact the heat balance of cattle.

Parameters that define a given environment include the following. The *dry bulb temperature* (DBT) is the temperature of the air taken with a standard thermometer that is shielded from direct sunlight. The *wet bulb temperature* (WBT) is the temperature read from a thermometer that is covered in a water-soaked muslin cloth over which air is passed, thereby recording the temperature of a parcel of air that has been cooled to saturation. The *black globe temperature* (BGT) measures radiant heat using a thermometer that is contained in the middle of a 15 cm diameter black metal sphere. The *wet bulb globe temperature* (WBGT) combines several of the above measures (dry-bulb, wet-bulb, and black-globe) into a single index that provides an index measure of the thermal environment. The WBGT index was originally developed to predict heat stroke in military personal[69] but has been adapted for many other uses, including the risk of heat stress in cattle.

Thermal indices

While most people associate heat stress with the ambient temperature, heat exchange between an animal and the environment depends on many factors other than the dry-bulb temperature. Attempts to capture the influence of those other factors have led to the development of several thermal indices that are mathematical constructs weighting various combinations of single measures into a combined measure that is designed to correlate with some outcome. Haldane[70] originally suggested that the wet-bulb temperature provided a better measure of human responses to hot conditions than did the dry-bulb temperature, and since then various indices have been adapted to animal applications where they have been used to predict the risk of heat (and cold) stress in animals.[71] Key indices that have been developed for cattle include the following: the *temperature humidity index* (THI; this combines effects of temperature and humidity), the *black-globe humidity index* (BGHI; incorporates temperature, humidity, and radiant heat), the *heat load index* (HLI; incorporates temperature, humidity, radiant heat, and wind speed/evaporative cooling), the *accumulated heat load units* (AHLU; accrues HLI scores above/below threshold as a summary of current heat load), the *equivalent temperature index for cattle* (ETIC; combines ambient temperature, relative humidity, wind speed, and solar radiation), the *comprehensive climate index* (CCI; adjusts dry bulb temperature by relative humidity, wind speed, and solar radiation), and the estimated *respiratory rate index* (RRI; this combines temperature, humidity, solar radiation, and wind speed to estimate respiratory rate – as a measure of heat stress risk). A recent review found that none of the thermal indices fully conformed with thermodynamic principles,[23] but the better indices correlated better with the physiological responses of cattle. Some indices were found to be more effective at predicting the temperature of a specific body site,[72] but this may not generalise to thermal stress. These were BGHI, RRI, THI, and CCI with the CCI showing the best correlation with rectal temperature. The challenge is to build an effective index that can differentiate effective from ineffective homeostatic responses, but that takes account of thermal inertia. It is unlikely that any single index will be applicable in all circumstances.

Factors and controls that can influence thermal homeostasis

Thermal homeostasis (homeothermy) depends upon the combined effects of animal metabolic, activity, including production-related heat generation, and the transfer of metabolic heat to the environment.[23] It is difficult to accurately predict the risk of thermal stress in individual animals from a single measure because many factors contribute to the risk that a given individual will be susceptible to thermal stress. Those factors include innate factors (such as species, breed, sex, genetics, and colour) and variable factors (such as acclimatisation, coat thickness, condition score, age, and health). The management of the risk of thermal stress can be aided by controlling those major risk factors, and using animals of an appropriate breed, class, acclimatisation status, nutritional status, condition score, and health. Once the best individuals are chosen, manipulation of the environment that those animals are exposed to can be optimised for the conditions, including the stocking rate, diet (amount and composition), access to shade, water (and the temperature of that water), bedding, and ventilation. Other strategies can also be implemented when conditions necessitate, such as wetting of the animals and/or the ground.

The way that many animal factors impact the risk of thermal stress is well known. As discussed earlier in this review, *Bos taurus* are less able to regulate their body temperature in hot conditions than *Bos indicus*.[8] Younger animals are less able to thermoregulate than adults.[65] Cattle in heavier body conditions tend to have a higher metabolic rate which makes them more prone to heat stress, but more resistant to cold stress, than their lighter peers. Those animals also carry more fat that can limit the movement of heat from the core to the periphery and then out of the body. Coat colour has an important effect on the absorption/reflection of solar radiation because darker coats absorb more solar radiation than white coats,[6] but the fate of radiant heat that is absorbed depends on the thickness and colour of the coat and the wind speed. Darker coats can end up with a lower absorption of radiant heat in windy conditions.[73] The thermal insulation that is provided by a coat depends on its thickness. *Bos taurus* coats tend to be thicker and more insulating than the coats of *Bos indicus*, and the latter tend to be more reflective to solar radiation. Coats are thicker in winter, which will impede heat loss, and the rate of sweating will be lower when cattle have not recently been exposed to heat, both of which will increase the risk of heat stress during winter in *Bos taurus*. A thicker coat also hinders the movement of water vapour from the skin, and this can impede evaporative heat loss across a winter coat. All the preceding means that a winter acclimatised beast will be susceptible to heat stress in conditions that might have no impact on a summer-acclimatised beast, and so strategies such as the minimisation of exposure to solar radiation via the provision of shade will be more important to prevent heat stress in winter acclimatised animals than in summer-acclimatised animals. The seasonal changes in the hair coat are caused predominantly by changes in the photoperiod, irrespective of latitude.[22] Lengthening days stimulate the replacement of the thick winter coat by a thin summer coat and vice versa. But nutrition can also influence coat development in that undernutrition stimulates the development of a winter coat. There are also genetic influences on coat characteristics,[74] and any advantage of a particular coat type on the risk of heat stress needs to be factored against other attributes that are influenced by coat structure, such as susceptibility to tick infestation.[75] The condition of the coat, and its thermal properties, can be impacted by the quality of manure management in lot animals and excessive coat contamination can reduce the ability of a coat to dissipate heat.[41,76,77]

Coat wetting can provide highly effective and rapid evaporative cooling, resulting in heat loss that can exceed that from sweating. The combination of wetting with enhanced ventilation of the area that contains cattle can be a key management intervention for cattle that experience severe heat stress.[78] In feedlot cattle, even a single wetting event resulted in a significantly lower peak body temperature (by around 0.3°C) and a reduction in the area under the temperature–time curve (i.e. shorter recovery times) compared to control cows.[7] The use of wetting needs to be judged against the conditions at the time because when the humidity is already very high, wetting provides no benefit and might even make the situation worse by increasing the ambient humidity. It is generally agreed that it is necessary to maintain wetting for the full duration of heat exposure to provide the most effective relief.[79,80] As we outline earlier in this review, the heat load from solar radiation can be the largest single component of the heat load on cattle, especially at more equatorial latitudes.[8] Shade is the best protection against radiant heat.[43] Cattle prefer shade over other options for cooling (such as wetting), and shaded heifers had higher feed intake and daily weight gain than did heifers who were sprinkled with water but not provided with shade.[5] While shade protects against direct sunlight, shaded animals can still be exposed to significant amounts of diffuse solar energy. Approximately 30% of the radiant heat load on cattle came from the sky, 20% from shade infrastructure, 20% from (outside) sunny ground, and 30% from shaded ground.[7] The height of a shade roof can have a significant effect on the radiant heat balance of cattle. While a higher roof reduces the overall radiant heat gain on cattle, it can result in greater exposure to direct solar radiation compared to low shade, while the lower shade will expose a cow to more indirect radiation from the infrastructure of the shade itself.[35] The most effective shade structures are a solid barrier (as opposed to shade cloth) that is reflective on the outside surface (such as white or silver) and dark on the underside surface, and ideally constructed using a shade material with low thermal conductivity (i.e. not metal). In general, the provision of larger airspace above cattle exposes them to cooler air. Effective roof venting is important to allow the escape of hot air.

Cattle are generally more tolerant to cold exposure than to heat exposure. A windbreak may be all that is required for pasture-based cattle in cold environments. The response of cattle in seeking protection against wind seems to be more correlated to wind speed than to ambient temperature.[16] Radiant heat loss to a clear sky on a cold night presents a major avenue of heat loss in exposed cattle. Because convective heat exchange depends on the wind speed, exposure to strong winds results in increased convective heat loss. Protection via shelter, the removal of drafts, and acclimatisation (thick winter coats) provide the best protection against night-time hypothermia. When cattle are lying, the thermal conductivity of the bedding impacts on the conduction of heat from the body. Cooled bedding for dairy cows has been shown to increase the conduction of heat from the body.[5]

Stock density impacts the environmental heat load. Metabolic heat from one animal can transfer to pen mates via conduction, convection, and radiation with the overall net transfer depending on the relative surface temperature of everyone. Because conspecifics will generally have a higher surface temperature than the surrounding environment, net radiant heat exchange from an individual will be reduced in close conditions. Sweating and respiratory evaporation also increase the water vapour pressure of the shared airspace thereby reducing the capacity for evaporative cooling. These effects can be controlled by managing stocking density and by controlling ventilation.

Because digestion, especially fermentation in the rumen, releases heat, the limitation or withholding of feed can help to reduce heat load, and to maintain body temperature during periods of high heat stress. Pre-cooling of water and feed can provide a heat sink and so reduce the heat load on cattle.[8] Similarly, feeding a low-fibre diet was associated with reduced standing time, increased lying time, and higher milk production in heat-exposed cattle.[81] Cattle exposed to cold-stress have an increased appetite which increases heat production in itself but also helps to meet the increased metabolic rate.[16] In contrast, cattle under heat stress enter negative energy balance when food intake decreases.[82] Reducing the fibre content of the diet can result in a reduction in heat generation from fermentation, and if the fibre is replaced by concentrate, it can help to ameliorate the negative energy balance. Feeding chicory was found to reduce body temperature in grazing dairy cattle under high heat challenge,[83] the mechanism of action suggested to be from lower fibre intake in the chicory versus the forage diet. Starch in the diet should be from grains that are slowly fermented in the rumen (e.g. oats, corn) to prevent spikes in digestive heat production.[84,85] The addition of extra fat or oil to the diet in heat-stressed dairy cows resulted in higher milk production, presumably as a result of the lower heat of digestion of fat compared to dietary protein and fibre.[86] Options for feeding include fats that bypass fermentation in the rumen (such as palmitic acid) and the calcium salts of fatty acids.

The rumen microbiome can be altered in heat-exposed cattle. One study identified a trend towards increased lactate-producing bacteria and decreased fibrolytic species within the rumen population after 6 days of exposure to elevated heat.[87] These microbial changes make cattle more prone to rumen acidosis. Rumen modifiers such as monensin can result in increased production of propionate and reduced production of acetate in the rumen, however, the outcomes of feeding monensin to heat-stressed dairy cows have been equivocal.[86] Reducing the protein content of the diets can reduce heat generation from the synthesis of urea.[88] Potassium (and other electrolytes) are lost in the sweat and bicarbonate is lost when saliva is lost via drooling. Increased insulin resistance is observed in heat-stressed cattle, especially dairy cows.[82]

Various studies have suggested that some additives can help thermoregulation during heat exposure. The addition of osmolytes such as betaine should help to stabilise cells (and reduce cellular sodium/potassium pumping) and therefore reduce the oxidative stress that can arise because of insulin resistance. However, no benefit from betaine supplementation was observed in Australian cattle feedlot studies.[89] The addition of vitamin E, niacin, selenium, salt, minerals as buffered metal ions, vitamin C, yeasts, GABA, or plant supplements (such as *Radix bupleuri*) have been previously examined, and the effects are often equivocal.[86]

Provision of sufficient water is essential. Cattle typically drink 10% of body weight as water per day, increasing to 20% under hot conditions. The temperature of the water provided for drinking does affect thermoregulation, more so for *Bos taurus* than for *Bos indicus*, however, the effect was not large. The provision of cool water (18°C) was observed to reduce the heat load by 3.0 MJ day^{-1} (125 kJ h^{-1}) compared to the provision of warm water (31°C), but that is less than 10% of the daily metabolic heat production in most cattle.[90] The location and accessibility of water troughs can be important because of dominance behaviour; a limited length or less accessible troughs allows dominant cows to limit access by recessive cows.

Conclusions

Cattle are homeotherms that have adapted to wide-ranging climates. Generally, *Bos indicus* have a lower metabolic rate and so more are tropical-climate adapted than *Bos taurus* which are more cool- to temperate-climate adapted. The rate of endogenous (metabolic) heat production varies between individuals and is influenced by breed, age, body condition, diet and level of acclimatisation. Selecting appropriate, acclimatised cattle for expected conditions can effectively limit the risk of thermal stress. Solar radiation is the major source of external heat for cattle, and often the dominant source of heat overall, especially in Australia. Radiant heat loss from cattle in cold, exposed (open skied) conditions can quickly result in cold stress. Adequate shelter/shade is often essential to limit heat- and cold-exposure in cattle. Radiant heat exposure from pen mates can also be a source of heat at higher stocking densities. Therefore, managing stocking density can limit the risk of thermal stress. Heat generation by digestion varies according to intake and dietary composition with a proportion of feed energy lost as heat during fermentation and digestion. The effectiveness of dietary additives on thermal stress risk mostly remains unproven, although some have promised on first principles. Additives that modify energy and electrolyte metabolism, stabilise cell membranes, assist with vasomotor control or provide antioxidant support may have limited heat and cold stress. Manipulation of the diet can help limit the risk of thermal stress in cattle. Cattle have limited ability to use radiation, conduction, and convection to dissipate surplus heat when the ambient temperature exceeds 36°C; only evaporative cooling remains effective for dissipating heat. Cattle can rely on sweating and respiratory evaporative mechanisms to dissipate heat for as long as water and electrolytes remain available. Evaporative cooling is less effective at high relative humidity (high water vapour pressure). Sprinklers and fans can be effective ways to increase evaporative heat loss in hot climates.

Cattle will often expose themselves to situations of excess heat and/or cold, where their efficient adaptive mechanisms can limit a temporary loss of homeothermy. Cattle also have significant thermal inertia and a variable circadian rhythm, making it difficult to use a single, defined body temperature to demarcate the point of loss of homeothermy. The response of cattle to heat exposure, and determination of the point where the welfare of those cattle becomes compromised, is best done by interpreting behaviour and physiological responses, including the type, severity, duration of response, and the timeliness and quality of recovery.

Management of the risk of heat- and cold-stress in cattle revolves around influencing endogenous heat production and controlling/aiding heat retention or dissipation. Interventions that minimise excess heat accumulation/loss and that provide for an effective recovery period (i.e. restore homeothermy) before the next environmental challenge are critical to limit or prevent adverse animal welfare due to thermal stress. These principles underpin effective management of thermal stress in farmed cattle.

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