

**COMPARISON OF THERMOREGULATORY MECHANISMS IN
HEAT SENSITIVE AND TOLERANT BREEDS OF *BOS TAURUS*
CATTLE**

A Thesis presented to
the Faculty of the Graduate School
at the University of Missouri – Columbia

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

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DECEMBER 2008

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ACKNOWLEDGEMENTS

I would like to thank my thesis committee for their guidance and support throughout my Master's program. Dr. Don Spiers for his advice and continuing guidance during my present and future studies. Dr. Tim Evans for his help and direction concerning the blood analyses and interpretation. Dr. Matt Lucy for his assistance and expertise in the completion of my program. Dr. Bob Weaber was instrumental in helping me bring together the experiment and working to get all the new technologies up and running.

Also I would like to thank my labmates, Peggy Ann Eichen, Laura Wax, Raja Settivari, Prakash Bommala, and all the lab 114 students who always kept things interesting regardless of what we were doing. Finally, I would like to thank all my friends and family for always being a support away from school whenever needed.

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Abstract

A study was performed to evaluate differences in thermoregulatory ability of two *Bos taurus* breeds with known differences in heat tolerance. Romosinuano (**RO**) is a tropically adapted breed. Nine Angus (304 ± 7 Kg BW; **AG**) and nine RO (285 ± 7.5 Kg BW) steers from USDA-ARS, Brooksville, Florida were transported to the Brody Environmental Center at the University of Missouri. Steers were housed for 14 d at thermoneutrality ($T_a = 21^\circ\text{C}$; TN) before initiation of heat stress. Heat stress (HS) consisted of daily cyclic T_a (26°C night T_a : 36°C day T_a) for 14 d. Steers were fed a typical feedlot diet at 1.6% of BW/d. Rectal temperature was measured with respiration rate six times daily. Sweat rates were recorded on specific days throughout the study on shaved shoulder and rump sites. Blood samples were taken once a week. Respiration rate at TN was higher ($P < 0.001$) in **AG** than **RO**, by ~ 20 BPM. There was a breed x time interaction ($P < 0.001$) at TN with the **AG** slowly adapting over time, and no reduction in **RO**. Angus steers also maintained rectal temperature 0.5°C higher than **RO** at TN ($P < 0.0001$). Sweat rates were slightly different at TN ($P < 0.04$). Both breeds initially increased sweat rate more than 4-fold during HS ($P < 0.0001$), followed by reduction after 7 d ($P < 0.0001$). Higher sweat rate was maintained in **AG** even after HS adaptation period ($P < 0.0001$). Both breeds increased respiration rate during HS, with **AG** steers exhibiting the higher rate ($P < 0.0001$), followed by a slight increase after 7 d ($P < 0.03$). Rectal temperature increased during HS for both breeds ($P < 0.0001$), but with a higher level in the **AG** breed ($P < 0.001$). There were breed differences for serum prolactin, leptin, creatinine, and cholesterol, with **AG** being higher than **RO**. Serum leptin increased for both breeds with HS. Although there were no breed differences at TN, **AG** steers

exhibited HS-induced increases in prolactin, creatinine, and cholesterol. However, these measures for **RO** were unaffected by HS. Romosinuano steers exhibit a lower level of heat loss than Angus steers during heat stress, while maintaining a lower core temperature. This suggests that lower metabolic heat production between these breeds is a key determinant of heat tolerance. The present study has identified additional physiological and endocrine markers that may aid in the identification of *Bos taurus* sensitivity to heat.

Key Words: Cattle, Heat, Tolerance

CHAPTER I

REVIEW OF LITERATURE

1. Introduction

One of the greatest challenges facing producers and livestock around the world is heat stress. Heat stress strongly affects animal bioenergetics, with adverse effects on the performance and well being of livestock. In addition, heat stress is a significant issue for grazing livestock or feedlot cattle where shade is not present or limited. Environmental factors such as ambient temperature, solar radiation, and humidity have direct and indirect effects on animals. Direct effects include reduced performance and reproductive ability. Indirect effects include changes in pathogen levels, as well as animal behavior such as lying in muddy stagnate water. Reduced feed intake, growth efficiency, and reproduction are all recognized results of heat stress (Kibler and Brody, 1951; Cartwright, 1955; Ingram and Mount, 1975). Although brief exposure to heat stress may have little effect on performance, problems can arise for cattle near market weight during sustained exposure to hot weather (Hahn, 1999). These periods of severe hot weather or heat waves occur almost annually, and in the United States are responsible for significant losses to the beef industry. Additionally, as green house gas emissions continue to accelerate and record ambient temperatures are recorded, it appears that global warming will continue to put heat stress at the forefront of problems for producers.

1.1. Economic losses

While there have been many breakthroughs in technology and management systems for heat stress reduction, there is still more progress to be made. Annual losses

average 897 million, 369 million, 229 million, and 128 million dollars for the dairy, beef, swine, and poultry industries, respectively (St-Pierre et al., 2003). Heat abatement programs (Shade, fans, etc.) have reduced the total economic losses from 2.4 billion to 1.7 billion dollars (St-Pierre et al., 2003). As we continue to select for high producing animals, there will continue to be problems with heat stress conditions. In the last 10 years, economic losses in the feedlot industry alone averaged 10-20 million dollars a year as a result of adverse climatic conditions. For each animal that dies from climatic stress, a corresponding economic loss approaches 5,000 dollars due to mortality and assorted animal performance losses. Across most of the US, gain loss is estimated to be 10 kg/yr or an additional 7 days in the feedlot (St-Pierre et al., 2003).

1.2. Fescue toxicosis and heat stress

As mentioned above, summer heat stress has a major impact on productivity of beef cattle found in many regions of the United States. Heat stress effects are exacerbated by consumption of an endophytic toxin (*Neotyphodium coenophialum*) resulting in a condition known as fescue toxicosis. Fescue toxicosis is common condition occurring during the summer months in southeast and midwest regions of the United States due to consumption of endophyte infected tall fescue (*Festuca arundinacea*). Over 90% of tall fescue pastures in US are infected with this fungal endophyte. The toxins produced by the fungus impact animal health resulting in hyperthermia during summer months along with reduced feed intake, average daily gain, and reproductive efficiency (Paterson et al., 1995). The beef industry is estimated to lose approximately \$600 million annually due to lowered conception rates and depressed body weight gains (Hoveland, 1993).

2. Thermal Balance

2.1. Homeothermy

All living organisms exchange heat with their external environment. Animals are divided into two groups: homeotherms or warm-blooded, and poikilotherms or cold-blooded animals. The difference between the two relates to their metabolic rate, with homeotherms having a heat production 7-10 times that of poikilotherms. This metabolic rate gives homeotherms the ability to regulate internal body temperature independent of ambient temperature within a certain range. Homeotherms evolved some 70 million years ago and are remarkably efficient at maintaining a relatively constant internal body temperature, even with the high energy diet needed to maintain the high metabolic rate (O'Reece, 2004). Homeotherms prefer an internal body temperature range from 33-40°C. A lethal temperature of most organs is between 43-45°C at which enzyme systems begin to denature. Homeotherms, such as cattle, utilize behavioral modifications as part of their method of thermoregulation. In addition, they are able to modify heat production and heat loss by physiological means. For internal body temperature to remain relatively constant, heat gain must equal heat loss. Heat exchange occurs via 4 different avenues: conduction, convection, radiation, and evaporation.

A rise of 1°C in internal body temperature in most species of livestock is sufficient to produce detectable changes in the number of physiological processes. In order for the animal to maintain thermal equilibrium, the net exchange of heat produced or gained from the environment must be equal to the heat loss to the environment, as indicated by the equation

$$\text{Equation 1: } M = \pm K \pm C \pm R + E \quad (\text{Robertshaw, 1985})$$

Where M equals the metabolic heat production, K is the heat exchanged by conduction, C is the heat exchanged by convection, R is the heat exchanged by radiation, and E is the heat exchanged by evaporation.

2.2. Heat Exchange

Heat exchange can be separated into 3 categories: heat production, non-evaporative heat loss, and evaporative heat loss. Non-evaporative is also referred to as sensible heat transfer because it is associated with the temperature differences of materials (Hansen, 2004). Evaporative heat loss is referred to as insensible heat exchange because it involves the latent heat of vaporization and change in the kinetic energy of molecular arrangement without a change in material temperature. Sensible is subdivided into heat exchange by conduction, convection, or radiation. Sensible heat exchange can be negative or positive (i.e., loss or gain) depending on the circumstance. Evaporative, on the other hand, only occurs in one direction, which is away from the body (i.e., heat loss). Although heat can be gained through conduction, convection, and radiation, ambient conditions only reverse heat flow into the body during peak summer temperatures. As skin temperature increases, the gradient between it and the core declines, slowing further heat transfer to the surface (McDowell, 1972). The consequence is the loss of thermal and vapor gradients between the skin and the environment resulting in reduced heat loss. If this condition persists, the accumulation of heat causes the core body temperature to rise as metabolic heat production continues resulting in hyperthermia.

2.2.1. Conductive Exchange

Conduction occurs within bodies and between objects in direct contact with each other. Conductive heat transfer (K) is defined as the net rate of heat transfer in a solid

material or a non-moving gas or fluid (i.e., by conduction) down a thermal gradient, within an organism, or between an organism and its external environment (IUPS Thermal Commission, 2001). Heat exchange by conduction at the skin may be expressed in units of watts described in the following equation showing its dependent on thermal conductance, surface area, and temperature gradient:

$$\text{Equation 2: } Q_k = (h_k) (A_k) [(T_1 \pm T_2) \div (d)] \text{ (Curtis, 1983)}$$

Where:

h_k is the thermal conductance ($h_k = K \cdot \Delta T^{-1}$; W/m²/°C), A_k is the surface area (m²) where the heat exchange occurs, $T_1 \pm T_2$ is the gradient in temperature, usually associated with skin temperature and the temperature of air or water, d is the distance between points T_1 and T_2 , and K is the thermal conductivity. Heat is transferred from higher temperature to lower temperatures through solid or liquid objects. Thus the amount of heat transferred is proportional to the magnitude of the temperature gradient. Since air has a low thermal conductivity in comparison with water, any air trapped against the skin reduces conductive heat exchange and acts as an effective insulator. The magnitude of heat transfer is dependant on the nature of the material in contact with the skin in conductive exchange, in particular its thermal conductivity. In the standing animal, the presence of a layer of air against the skin means that most of the heat transfer takes place to air, and since air has a poor thermal conductivity and lower specific heat than water, conductive heat transfer plays a small role in the total heat with the environment (Roberstshaw, 1985).

2.2.2. Convective Exchange

Heat gain or loss by convection is achieved by the movement of fluid or gas in contact with the skin as well as transfer of heat that accompanies respiration. Convective heat transfer (C; Equation 1) is defined as the net rate of heat transfer in a moving gas or fluid (i.e., by convection) between different parts of an organism, or between an organism and its external environment (IUPS Thermal Commission, 2001). It may develop and be amplified by thermal gradients and by forces such as wind, fans, pumps or body movement, and usually expressed in terms of unit area of the total body surface (IUPS Thermal Commission, 2001). These two categories of convective exchange are free convection and forced convection. Free convection occurs as fluid in contact with the surface is heated which changes the density and causes it to move away replaced by cooler fluid. Forced convection occurs due to external forces (winds or fans) not by local heating. During the winter time, when wind chills are high, forced convection heat loss is sometimes high enough to cause hypothermia.

Convective heat transfer is described in the following equation as:

$$\text{Equation 3: } Q_h = (h) (A_h) (T_a - T_s) \text{ (Curtis, 1983)}$$

Where: h is the coefficient of convective heat transfer ($h_c = C \cdot \Delta T^{-1}$), A_h is the animals surface area that is affected by convection, T_a is air temperature, and T_s is the skin or surface temperature. Convective heat exchange is similar to conduction in that it is driven by the temperature gradient.

2.2.3. Radiative Exchange

Radiation is the only means by which heat flows without the aid of a material medium allowing it to pass through a vacuum. Radiant heat exchange (R; Equation 1) is defined as the net rate of heat exchange by electromagnetic energy between an organism

and its environment, and is usually expressed in terms of unit area of the total body surface, i.e., as a heat flux (IUPS Thermal Commission, 2001). This avenue of heat exchange is described as:

$$\text{Equation 4: } Q_r = A_r \sigma [(aT_e^{-4}) - (eT_s^{-4})] \text{ (Curtis, 1983)}$$

Where: A_r is the effective radiative surface area of the animal (m^2), A is the absorptivity of the animals surface for thermal radiation, σ is Stefan-Boltzmann constant, T_e is the average absolute temperature of animals radiant environment ($^{\circ}K$), E is the average emissivity of environmental surfaces for thermal radiation, and T_s is the average absolute temperature of animals radiant surface ($^{\circ}K$). Heat exchange by radiation involves transfer of heat via electromagnetic waves and consists of heat transfer within the visible and infrared portions of the spectrum. Within the visible spectrum of 0.38–0.78 μm wavelengths, the amount of heat transfer is determined by the color of the surface. A black surface has an absorbance of 1. The heat gain within the visible light is derived entirely from the sun and is referred to as solar radiation. Heat exchange in the infrared spectrum (i.e., 0.78–100 μm wavelengths) is independent of color and is referred to as thermal radiation. Heat transfer in this way occurs by the emission of electromagnetic waves which transmits energy away from the emitting object. Any two objects that “see” each other radiate toward each other with the net direction depending on the surface-temperature gradient (Curtis, 1983). In general, heat is gained within the visible spectrum by the animal and lost in the form of thermal radiation.

2.2.4. Evaporative Exchange

When the environment is cooler than the animal’s surface, temperature gradients allow for the previous 3 avenues of temperature transfer. However, as environmental

temperature rises closer to body surface temperature, the animal must invoke evaporative heat loss. Evaporative heat loss is relatively independent of temperature, depending mainly on a vapor-pressure gradient. Evaporation of a liquid occurs when liquid molecules have sufficient energy to overcome cohesive forces and escape from the liquid surface into the environment (Curtis, 1983). Evaporative heat transfer (E) is defined as the rate at which heat energy is transferred by evaporation from or condensation on the skin and the surfaces of the respiratory tract, and usually expressed in terms of unit area of total body surface (IUPS Thermal Commission, 2001). The equation for evaporative heat loss is:

$$\text{Equation 5: } Q_e = (\lambda) (A_w) (d) (E_a - E_s) \text{ (Curtis, 1983)}$$

Where:

λ is the water's latent heat of evaporation at the surface temperature, A_w is the wet area of the animal's surface, d is the evaporative diffusion coefficient, E_a is the vapor pressure of air, and E_s is the vapor pressure at the evaporation surface. Air speed becomes important for this avenue of heat loss with air carrying vapor away from the surface and thus maintaining a high vapor pressure gradient in the surface surrounding the animal. Relative humidity is also an important factor.

2.3 Thermoregulatory Profile

While animals continually lose and gain heat from their environment, they do not need to alter their behavior or physiology to maintain internal body temperature during certain ranges of ambient temperature. This range is known as the thermoneutral zone (TNZ). The TNZ is defined as the range of ambient temperature at which thermoregulation is achieved only by control of sensible heat loss, i.e., without regulatory

changes in metabolic heat production or evaporative heat loss (IUPS Thermal Commission, 2001). The TNZ changes with body size, insulation, posture, resting metabolic rate, and basal metabolic rate (BMR) vary (IUPS Thermal Commission, 2001). Species, breed, age, gender, degree of thermal acclimation, and time of day all alter the limits of the TNZ zone (Yousef, 1985). For instance, the TNZ is narrow for young animals and wider for adult animals of the same species.

As the ambient temperature reaches the limits of the TNZ, it approaches the lower and upper critical temperatures to define the TNZ. Lower critical temperature (LCT) is the ambient temperature below which the rate of metabolic heat production of a resting animal must be increased by shivering and/or nonshivering thermogenesis in order to maintain thermal balance (IUPS Thermal Commission, 2001). Upper critical temperature is the ambient temperature above which the rate of evaporative heat loss of a resting thermoregulating animal must be increased (e.g., tachypnea or sweating) in order to maintain thermal balance (IUPS Thermal Commission, 2001). Upper critical temperature (UCT) has also been used to define the ambient temperature above which the mechanisms of heat transfer to the environment of a resting animal are exceeded and the core temperature is forced to rise and, as a consequence, metabolic energy transformation, i.e., the internal heat load, is further increased (IUPS Thermal Commission, 2001).

3. Short-term physiological responses to heat stress in cattle

3.1. Thermal input and controls

An animal's initial response to heat stress consists mainly of increasing heat loss. Information on internal and skin temperatures is sensed by specialized nerve receptors or thermoreceptors that are located throughout the body (Curtis, 1983). It is known that body surface temperature is measured by cutaneous thermal sensors and core temperature by thermosensitive structures within the preoptic anterior hypothalamus (POAH), brain stem, spinal cord and other places (Curtis, 1983). Some receptors are sensitive to increasing temperature (warm receptors) and others to decreasing temperature (cold receptors). These two broad classes of neurons have opposite responses. Warm receptors increase their firing rate in response to an increase in temperature, while cold receptors increase their rate of firing to a decrease in temperature. These two types of thermosensors are found throughout the body including the brain, spinal cord, and in the skin (Blumberg, 2002). It is the integration of these multiple sources of information by the brain that ultimately triggers a behavioral or physiological response.

Regulation of body temperature depends on the nervous system's ability to sense and integrate information from the external environment and deep within the body core. The hypothalamus is considered to be the key region for controlling body temperature (Ingram and Mount, 1975). The hypothalamus is sensitive to local temperature and also contains cells that play an important part in control of body temperature (Ingram and Mount, 1975). It has been shown that if the preoptic region of the hypothalamus is destroyed, the animal is unable to regulate internal body temperature in a hot environment, but still regulates during exposure to cold (Clark et al., 1939). Electric stimulation of the anterior hypothalamus results in vasodilation and panting even in a thermoneutral environment (Anderson et al., 1956). As previously stated, there is

evidence that other regulatory centers also influence body temperature regulation although they seem to lack the fine control necessitated by the hypothalamus. For instance, heating and cooling the spinal cord elicits the same response as heating or cooling the hypothalamus. However, this response can be altered by the hypothalamus. Heating or cooling the spinal cord and the hypothalamus together results in an enhanced change in body temperature. Heating or cooling the spinal cord and doing the opposite to the hypothalamus results in a reduced change or dampened effect (Ingram and Mount, 1975). Heating and cooling the abdomen has also been shown to activate thermoregulatory mechanisms suggesting a concentration of thermosensitive cells in this region (Rawson and Quick., 1970).

3.2. Behavioral changes

Although many animals have special heat loss mechanisms that enable them to control their body temperature, such as sweating or panting, these activities involve the use of stored energy and water. Modifications of behavior patterns or behavioral thermoregulation, however, may be adequate to enable an animal to maintain acceptable comfort levels without involving these mechanisms. The simplest behavioral modification involves an animal changing their orientation to the direction of the wind or sun (Cabanac, 1975). Cattle will also bunch together to obtain shade from each other as a natural herding response when under stress (Meat & Livestock Australia, 2006). Ansell (1981) found that cattle under heat stress refuse to lie down; suggesting that the need of the animal is to expose as much of the bodies surface as possible to the atmosphere. Standing in lakes or streams is also utilized as a behavioral change to increase conductive heat loss to water in order to reduce heat stress. Water has a higher specific heat than air

and, as a result, is a superior heat sink. When cattle were exposed to heat they frequently sprinkled drinking water over their bodies (Ragsdale et al., 1951). Cattle may also dunk their muzzles into the water without drinking in an attempt to shed body heat.

One of the most common behaviors observed in heat stressed cattle is to seek shade to reduce solar radiation. Research indicates that certain breeds of cattle will begin to seek shade when the ambient temperature exceeds 20°C, although similar cattle that are adapted to hot environments may not seek shade until the ambient temperature is approximately 28°C (Meat & Livestock Australia, 2006). It appears that natural shade, such as trees, are their first preference, however if only artificial shade structures are available they will choose the structure that provides the highest protection from the sunlight (Meat & Livestock Australia, 2006). It is known that exposure to ambient temperature above 24°C reduces the time that cattle spend grazing and causes them to spend longer times in the shade (Whittow, 1971). Cattle have also been shown to graze for longer periods at night than during the day under periods of heat stress (Payne et al., 1951). In fact, Seath and Miller (1946) reported that during the day when dry bulb temperature was 29°C cattle spent 11% of the time grazing, but during the night when temperature was still 27°C (but no solar radiation), cattle grazed 35% of the time. Studies looking at feedlot cattle have shown similar results to pasture. Animals spend more time in the shade and less time feeding. Castañeda et al. (2004) found that in unshaded feedlots, animals spent more time standing at the water trough than shaded animals. This is not necessarily an indicator of increased water intake, as it is believed that this behavior is done to cool their heads, as water evaporating from the trough will lower the ambient temperature immediately above it (Meat & Livestock Australia, 2006). Food and

water intakes are greatly affected by heat stress and will be discussed in the coming paragraphs.

3.3. Metabolism

The main source of body heat accumulation in cattle is metabolic heat (Meat & Livestock Australia, 2006). This is heat produced within the body (ingested or stored energy) for every biochemical reaction associated with any body function, including maintenance and production needs such as pregnancy, lactation, and growth (Meat & Livestock Australia, 2006). Under cold conditions, metabolic heat production can be of value in maintaining body temperature; however, under hot conditions, metabolic heat must be dissipated from the animal. In fact, metabolism generates about one third of the heat load of a cow standing in a hot radiant environment (Finch, 1986). In the resting animal, a large portion of this metabolic heat load is maintained in the core and must be transported by the blood to the skin and extremities where it is transferred to the animal's surroundings. If homeotherms are unable to transfer adequate heat to their surroundings, it can build up in the body leading to hyperthermia. Cattle that adapt to hot conditions usually do so by decreasing heat production or increasing heat dissipation (McDowell, 1972) to result in the maintenance of homeothermy. Increasing heat dissipation is usually sufficient when the heat load is of short duration (1–2 days) (Meat & Livestock Australia, 2006). However, if heat stress conditions continue, cattle must reduce heat production to control their core body temperature (Finch, 1986). This is achieved by a reduction in feed intake. There is some controversy on what is the ultimate cause of the reduction in metabolism and feed intake. It is widely accepted that feed intake “drive” is somehow related to the energy/oxygen metabolism of the animal (Gill and Romney, 1994).

However, whether the reduction in feed intake is caused by a reduction in metabolism or does a drop in metabolism drive down feed intake.

3.4. Feed intake

Food intake by the animal is directly related to all aspects of energy metabolism with the release of heat for maintenance, activities, and production (Finch, 1986). Purwanto et al. (1990) concluded that total heat production within the animal is dependant, in part, on dry matter intake. High feed intake increases metabolic rate and water intake which gives rise to a need for a greater heat loss effort. When environmental temperature increases above the thermoneutral zone, the metabolic rate also increases as a result of the increased body temperature and Q_{10} effect ($Q_{10} = (K_2/K_1)^{10/(T_2-T_1)}$; Whittow, 1971). The temperature coefficient or Q_{10} effect represents the factor by which the rate of a reaction increases for every 10-degree rise in the temperature (T). The rate of the physiological process is measured at two different temperatures, T_1 and T_2 (where $T_2 > T_1$). If the rate of the reaction is completely temperature independent, it can be seen from the equation above that the resulting Q_{10} will be 1.0. If the reaction rate increases with increasing temperature, Q_{10} will be greater than 1. Thus, the more temperature dependent a process is, the higher will be its Q_{10} value. This gives rise for a need to reduce feed intake. The reduction in feed intake is followed by a reduction in metabolic rate, therefore reduced maintenance, which helps balance heat production with heat loss (Turner and Taylor, 1983). The connection between reduced feed intake of cattle and increased environmental temperature is only partly understood. It is believed that the hypothalamus acts as an integrator for regulating feed intake and other functions of energy balance (Bianca, 1965). This hypothesis has been proven in goats by (Anderson et

al., 1956) who found that warming the pre-optic area of goats with thermodes caused hungry goats, which had just began to eat, to stop eating within 1 minute.

The extent to which feed intake is reduced due to changes in body or ambient temperature varies in the literature with almost all research done in this area under short term exposure Bianca et al. (1965) showed a significant decrease in feed intake of steers housed at 40°C, while water intake increased twofold. Kibler et al. (1965) found at 29°C that feed intake dropped by 10-25% in cattle. Johnson et al. (1966) noted a similar drop at 31°C in cattle. Conrad (1985) reported that not until ambient temperature reaches 25°C does a reduction of feed intake occur in cattle, but with only found a 3-10% drop between 25 and 35°C. This reduction in feed intake is also dependant on type of feed, air temperature, thermal radiation, but is ultimately related to body temperature. Yousef et al. (1968) found that the reduction in feed intake of cattle was less at higher air velocities, and when intensity of thermal radiation was lower suggesting that skin temperature may play a role as an input to feed intake. Cattle on high energy grain diets (consistent with a higher heat of digestion) may reduce dry matter intake by more than 25% and once high heat load conditions abate, may not return to previous levels of DMI (Meat & Livestock Australia, 2006). Cattle on low quality roughage (low energy) diets experience variable intake reductions, often around 10%, and are more likely to return to full feed when conditions return to normal (Meat & Livestock Australia, 2006). If ambient temperatures above UCT persist, cattle will acclimate to the conditions after about a week days of exposure provided they do not overheat.

3.5. Mechanisms of heat exchange

Cattle are considered to be homoeothermic in that body temperature over a wide range of environmental extremes. To maintain internal body temperature within narrow limits requires sensitive and quick quick-acting mechanisms which balance any changes in heat production. The rate of heat transfer from an animal to the surrounding environment is dependant on the temperature and vapor pressure gradients. The influence of the thermal environment on an animal is primarily exerted through energy exchanges which involve convection, conduction, radiation, and evaporation.

3.5.1. Conduction

Conduction has two primary roles within cattle. It is partially responsible for the movement of heat from the core to the skin surface and the flow of heat from the periphery to surrounding objects in contact with the skin surface. Therefore, conductive heat flow to the surrounding in cattle mainly applies to ground contact. When standing, the heat transfer with the ground has to occur through the animal's feet; which constitutes only 2% of the body surface area (Meat & Livestock Australia, 2006). In cattle and other hoofed animals, the distance between the blood vessels and surface is much greater than those of non-hoofed animals; therefore the amount of heat transfer is due to the thermal conductivity of the hoof (Robertshaw, 1985). If an animal is lying on a cool or wet surface when as much 20–30% of the body surface may be in contact with the ground, conductive heat transfer will be much greater and depend on several variables including: thermal conductance, temperature gradient, and area of contact (Meat & Livestock Australia, 2006). However, conduction is of minor importance of heat dissipation for cattle during heat stress due to the reduced thermal gradient (McDowell, 1972).

3.5.2. Convection

Since cattle are not aquatic animals, they lose heat to the environment using air as the medium. Anything that resists movement will decrease the rate of convective heat transfer. Since cattle are furred animals, the fur entraps a layer of air close to the skin and tends to resist passive or natural convection (Robertshaw, 1985). In most conditions, passive convection is of little importance to cattle. However, forced convection tends to break up the layer of air retained by the fur and increases convective heat transfer to the environment. Convection also plays a key role in respiratory heat loss. The enhanced air flow through the nasal passages and upper respiratory tract can carry a large amount of body heat. The inspired air is not only humidified, but adjusted to core body temperature by the time the air reaches the trachea (Robertshaw, 1985). Heat transfer within the cow is accomplished by combination of heat distribution using blood and conduction from warmer tissues within the thoracic cavity.

Convective heat transfer by circulation is the main mode of heat transfer to the periphery of livestock. Increasing blood flow to the skin caused by vasodilation increases the thermal gradient between the skin surface and air prompting heat loss to the surroundings (McDowell, 1972). The adjustment of skin temperature to meet the needs of temperature regulation occurs primarily in the extremities; whereas variation in the trunk region is very small (Ames, 1970). Hales (1973) reported in sheep that at thermoneutral, approximately 1% of the cardiac output transverse anastomoses, however this increases up to as much as 14.5% during heat stress. Arteriovenous anastomoses are blood vessels that connect an arteriole directly with a venule. These structures serve as low-resistance blood shunts past capillary networks during heat stress. In the heat, the peripheral drain the capillary beds into the skin. Changes in the caliber of peripheral blood vessels are

accompanied by changes in various cardiovascular functions such as an increase total vascular volume and thus a decline in blood pressure.

3.5.3. Radiation

Radiant heat transfer is the transfer of heat by the exchange of electromagnetic waves. These waves are broken up into short-waves or waves from the sun and long-waves which radiate from the environment. Studies on the heat exchange in the long-wave portion of the spectrum indicate that the net transfer is away from the animal (Robertshaw and Finch, 1976). The magnitude of radiant heat transfer is very complex. Exposure is a function of direct sunlight to the surface of the animal, as well as the amount reflected from the ground. This is dependant on the color and presence or absence of vegetation on the surface. In addition, some sunlight is scattered by dust and particles in the atmosphere. For the most part, solar radiation in cattle is a function of surface area exposed to the radiation, and the color and structure of their coat (Robertshaw 1985).

A black coat has an absorbance of nearly 1.00 whereas white fur has an absorbance of 0.37 and red fur of 0.65 (Cena and Monteith, 1975). Since cattle have posses a hair coat, the primary site of absorption of radiant heat is the surface of the hair. The intensity of solar radiation that reaches the earths surface varies, but under clear skies often reaches values of about 1000 W/m^2 on a plane perpendicular to the solar beam (Walsberg, 1983). Of this beam, roughly one-half of this energy lies in visible wavelengths, and hence is of sufficient magnitude that coat color might significantly modify an animal's heat balance (Walsberg, 1983). Many studies have been conducted to look at the effect of solar radiation on heat gain in cattle. Da Silva et al. (2003) found that

light colored hair coats have reflectance values much greater than those of dark colored hair coats for the wavelengths from 300-850 nm. However, they found that Nelore cattle, which have a mixture of white and dark hairs, had a higher reflectance value than white cattle for the wavelengths from 300-600 nm. They also determined that grey colored coats reflect better than red colored coats (Da Silva et al., 2003).

While this gives a general understanding of radiant heat gain, it is not the full story. Skin color has also been shown to play a role. Non-pigmented skin has a reflectance level that is lower than light grey skin, especially for the wavelengths in the range of 300-600 nm. Red and brown skin have reflectance levels close to those of black and gray skin in the same range, however beyond 600 nm the values increase for red/brown skin but remain constant for darker skin (Da Silva et al, 2003). Another issue with solar radiation becomes coat structure. There are only a handful of studies that consider this. Cena and Monteith (1975) determined that number of hairs, length, diameter, and the angles relative to incident of radiation are all key factors that are unaffected by coat color.

3.5.4. Evaporation

Under hot conditions, the amount of heat that can be lost via conduction, convection, and radiation is limited. Moreover, when the ambient temperature and the radiant temperature are above or equal to skin temperature, evaporation is the only avenue available for cattle to lose heat (Collier, 2007). The vaporization of water from the body takes place from the respiratory tract and through the skin via sweating. Though respiration and sweating are under control of the animal, water loss through the skin by

passive diffusion is constantly occurring and not subject to control. However, both panting and sweating undergo tremendous change during heat stress.

3.5.4.1. Respiration

In some animals such as man the control of respiration is mainly directed only toward elimination of carbon dioxide from the tissues and provision of oxygen. However in cattle and other animals during heat stress, respiration is directed toward evaporation of moisture from the respiratory tract. In cattle, this increase in respiratory rate (panting) is associated with heat exposure involves an increased ventilation of the dead space (Robertshaw, 1985). This is achieved by increasing the frequency and decreasing the tidal volume (Robertshaw, 1985). Cattle pant with their mouth closed causing heat exchange to take place at the mucosa of the upper respiratory tract. Heat is provided by the blood supply to the nasal mucosa and the cool blood drains into the venous sinuses at the base of the skull (Robertshaw, 1985). At higher rectal temperatures the respiratory rate declines while tidal and minute volumes increase. This further increase in minute volume ensures that respiratory evaporation continues to increase, inspite of the fact that the increase occurs at the expense of an over-ventilation of the alveoli (Whittow, 1971). This ultimately leads to blood levels of carbon dioxide to fall to very low levels and increasing blood pH (Whittow, 1971). A transition from rapid, shallow breathing to a slower, deeper type of respiration appears to represent a physiological mechanism permitting maximal respiratory evaporative cooling with minimal disruption of the blood gases (Whittow, 1971). The last phase of respiratory frequency is open-mouthed panting, with the tongue protruding, and coincides with the peak respiratory rate and may be dictated by considerations of airway resistance.

Respiratory rate has long served as an indicator of heat load and heat strain on the animal during hot weather. Respiratory rate increases as stressors cause an animal to maintain homeothermy by dissipating excess heat when other avenues (ie., Conduction, convection, radiation) become inadequate (Hahn, 1999). The normal range of respiration rate for cattle at thermoneutrality is 30 to 60 bpm (Smith, 1996). A respiration rate of 80 to 120 bpm is indicative of cattle under moderate to high thermal stress, whereas above 120 bpm is considered to be an excessive heat load (Mount, 1979). Respiratory rate is influenced by ambient temperature, solar radiation, relative humidity, and wind speed. Of these, ambient temperature has been identified as the most important influential (Hahn, 1999). Hahn et al. (1997) found that respiration rate showed a strong correlation with ambient temperature once it surpassed 21°C, and increased at a rate of 4.3 bpm per °C above a baseline of 60 bpm. Respiratory rate eventually hits what is known as a ceiling characterized by a shift from rapid shallow breathing to slower open mouth panting. Cattle have been shown to anticipate temperature changes such as a tendency to decrease respiration rate prior to a decrease in ambient temperature (Gaughan et al. 1999). Gaughan (2002) concluded that a decreasing respiration rate with rising ambient temperature is not always indicative of an animal coping with the hot conditions, but may indicate a failure to cope. While most studies have looked at respiration rate, the panting score as defined by Meat & Livestock Australia (2006) book may, in fact, be a better indicator of thermal strain. While evaporative cooling is utilized by panting, it is not as effective as sweating.

3.5.4.2 Sweating

There has been much controversy in regard to sweating in cattle. The amount of sweat produced by each sweat gland in cattle is much less than that of humans (Robertshaw, 1985). Therefore, the amount of sweat produced per unit of surface area is less and the skin rarely appears wet. This led many researchers to state that cattle are not a sweating species (Worstell and Brody, 1953). It took the work of Dowling (1958) to clearly demonstrate that sweating in cattle is important for thermoregulation. By putting plastic coats which prevented vaporization of skin moisture over their bodies and walking them for one hour during the summer heat, he found that their core temperature rose faster and higher than control animals.

There are two types of sweat glands. Those that open on the surface of the skin by means of a duct which is arranged in a spiral fashion through the epidermis are defined as eccrine. Whereas, the glands associated with hair follicles and whose ducts open into the hair follicle closer to that of the sebaceous glands are referred to as apocrine (Ingram and Mount, 1975). While humans possess both eccrine and apocrine sweat glands, cattle only possess apocrine (Findlay et al., 1950; Dowling, 1955; Nay and Hayman, 1956). The apocrine glands are controlled by the alpha-adrenergic system, in contrast to those in horses which are beta-adrenergic and humans which are cholinergic (Findlay and Robertshaw, 1965). Interestingly, no nerve supply has been detected histologically in cattle, although it is known that an intact nerve supply is essential for sweat gland function (Jenkinson et al., 1966). In a later study, Jenkinson (1978) found no sudomotor nerve supply with even an electron microscope. It appears that a fibrous capsule exists around the sweat glands and no nerves have been able to penetrate the capsule (Robertshaw, 1985). However, it is thought that since there is a close anatomical

association of capillary beds with sweat glands that the amount of blood directed to these capillary beds may affect of rate of sweat production in cattle during heat stress (Schleger and Bean, 1971). While some controversy does exist as to the exact mechanism; sweating is a very effective avenue of heat loss accounting for 70-85% of maximal heat loss (Kibler and Brody, 1952; Finch 1986).

The total number of sweat glands is determined at birth. However, it is very well documented that there are regional anatomical differences in sweat glands. Findlay and Yang (1950) found that the ventral region of the neck and trunk had the greatest number of sweat glands, while the forehead and legs showed the lowest numbers in Ayrshire dairy cows. They determined the average number of sweat glands per square cm to be 1,871. It is not clear whether the rate of evaporation depends solely on the number of glands or is due to the functional capacity of sweat glands within each region. However, regional sweat rates have been extensively studied. Volcani and Schindler (1954) measured relative rates of moisture vaporization and found an order of diminishing evaporation from face, shoulder, neck, dewlap, back, rump, thigh, and abdominal regions. Berman (1957) gave the order as the neck, front flank, back, thigh, forehead, and abdominal regions. McDowell et al. (1955) suggested that the order be from neck, trunk, dewlap, legs, and mid-belly line. There is broad agreement between the rankings of the regions given by all observers that the shoulder regions possess greater sweat gland numbers compared to the rump regions. Because many of these studies used different breeds, it seems likely that the regional distribution of cutaneous evaporative heat loss is similar across a variety of cattle breeds (McLean, 1963). McLean (1963) reported that the

moisture evaporated from the skin is more related to the functional ability of the glands than their distribution over the skin.

Little is known about the composition of sweat from the skin of cattle. In one of only a few studies, Johnson (1970) reported that the amounts of sodium and potassium in sweat are very small, but variable at an air temperature of 20°C. However, he noted a significant increase as air temperature rose to 45°C. At this temperature, the collected sweat contained at least four to five times more potassium than sodium. Even with this increase, the total sodium and potassium loss through the skin totaled no more than 13% of the sodium and potassium in the feed, and did not result in changes in either plasma sodium or potassium concentrations. This study also found that there are no significant differences in electrolytes from sweat between breeds or between different sites of collection.

3.6 Endocrine responses

Both acute and chronic thermal stress requires metabolic adaptations to accommodate altered nutrient utilization caused by stress. Due to the considerable involvement of the endocrine system in the coordination of hormone concentration of metabolism, it is not surprising that thermal stress results in alteration of hormone concentrations in the blood (Beede and Collier, 1986). Hormones involved in adaptation to thermal stress include thyroxine (T₄), triiodothyronine (T₃), glucocorticoids, antidiuretic hormone, aldosterone, prolactin, and growth hormone (Beede and Collier, 1986).

It has also been recognized that thyroid hormones increase oxygen consumption of tissues and, as a result heat production. Thyroid activity is reduced under heat stress

conditions (Beede and Collier, 1986; Silanikove, 2000). The response of concentrations of T_3 and T_4 to heat stress is slow and it takes several days for levels to reach a new steady-state (Silanikove, 2000). This is not an immediate response to acute heat stress, but instead is involved in the acclimatization of animals to a sustained heat load. A decrease in thyroid hormone level is correlated with a decrease metabolic rate and a reduction in cellular heat production (Beede and Collier, 1986). It is not clear whether the reduction in T_3 and T_4 is due to thermal inhibition of the hypothalamus or lower feed intake and metabolism (Johnson, 1985).

Unlike many hormones, growth hormone does not function through a target gland, but it affects almost all tissues of the body. Growth hormone is produced by the anterior pituitary gland and has been implicated in nutrient partitioning as well as initiation and maintenance of lactation (Beede and Collier, 1986). Growth hormone concentrations decline with both short- and long-term exposure to heat (Johnson, 1985). This decrease is not well understood, but is thought to be due to thermal inhibition of the hypothalamus or lowered feed intake and metabolism (Johnson, 1985).

Prolactin, which is similar to growth hormone is also produced by the anterior pituitary gland. Prolactin concentrations increase during acute thermal stress (Wetteman and Tucker, 1974), but like other endocrine responses, it is not well understood why (Johnson, 1985). However, Beede et al., (1982) and Collier et al. (1982) indicated that increasing dietary K from .64 to 1.08 or 1.64% markedly reduced plasma prolactin in heat-stressed cattle, suggesting that prolactin may be involved in potassium and sodium turnover during thermal stress.

Epinephrine and norepinephrine concentrations are elevated during both acute and chronic thermal stress (Alvarez and Johnson, 1973). This is likely related to increased sweat gland activities which are alpha-adrenergic in nature and are known to stimulate sweat secretion (Bianca, 1965). This would support other research that sweat glands of cattle are not innervated directly (Jenkinson et al., 1966), but are under adrenergic regulation (Joshi et al., 1968; Allen and Bligh, 1969).

The majority of acute endocrine responses to thermal stress are associated with altering water and electrolyte turnover. This response is necessary to comply with the increase in evaporative water loss which is the major route of heat exchange when ambient temperature approaches body temperature (Collier et al., 1982). Increases in vasopressin concentrations are associated with the need to conserve water and increase water intake to offset water losses in the respiratory tract and skin (E1-Nouty et al., 1980). Increased water turnover requires associated increases in electrolyte turnover to move water through various fluid pools to the evaporative surfaces (Beede and Collier, 1986).

Accordingly, thermal stress imposes a need to conserve electrolytes, specifically potassium in ruminants. Aldosterone is a steroid hormone secreted by the adrenal cortex that causes re-absorption of sodium and, concomitantly, a large flux of water at the level of the kidney. Heat stress in cattle is associated with a decline in plasma aldosterone concentrations (EL-Nouty et al., 1980; Collier et al., 1982; Johnson, 1985). EL-Nouty et al. (1980) suggested that the decrease in serum potassium may be the main factor inhibiting aldosterone release during heat exposure. This decrease in aldosterone level during heat exposure may be the main factor contributing to the increase in urine output.

The decline is associated with the reduced concentrations of Sodium and potassium in the blood serum and of potassium in the urine. However, urinary Sodium excretion increases, perhaps to aid in the conservation of potassium as it was lost via cutaneous evaporation.

4. Long-term physiological responses to heat stress in cattle

4.1. Adaptation

Adaptation is defined as a change which reduces the physiological strain produced by a stressful component of the total environment (Yousef, 1985). The magnitude of environmental stress can only be measured indirectly through the response of the animal. The acute response may be a measurement of the strain due to stress. After consistently longer periods of stress, the measurable response is probably a product of adaptation (Scott, 1981). Adaptation may involve physiological shifts in the animal within its lifetime to the environment or genetic adaptation that involves forces of selection across generations. It may be confined to a small area of tissues or it may affect the entire animal. Adaptation can be broken down into two subcategories: acclimation and acclimatization. Acclimation is a physiological change occurring within the lifetime of an organism, which reduces the strain caused by experimentally induced stressful changes, in particular climate factors (Yousef, 1985). Acclimatization, which is also a physiological change that occurs within a lifetime, reduces the strain caused by stressful changes in natural climates such as seasonal changes. Adaptation to hot environments can involve physical, behavioral, physiological, and morphological changes.

4.1.1. Physical

Physical changes are brought about through genetic selection or heritable characteristics that are transferred from generation to generation. Subtropical cattle have dewlaps and longer limbs than temperate cattle. The dewlap has been considered to act as a heat dissipater by adding to an animal's surface area. This increase in surface area allows for more sensible heat flow to the environment. It has also been found that animals adapted to hot environments have different skin colors and may be able to change their color over time to alter the absorption of solar radiation. It has also been shown that in less heat adapted cattle there is a greater layer of subcutaneous fat and thermal insulation that may lead to a poorer heat tolerance. One of the most noticeable changes brought about by long-term exposure to heat is a change in coat characteristics such as color and length.

As discussed in detail for short-term heat stress, coat color and consistency has a major impact on radiative heat flow. Brody (1956) determined that cattle coats tend to be light-colored in the tropics to better reflect solar radiation, thus keeping the animal from becoming overheated. He reported that cattle undergo summer lightening and winter darkening of their hair to alter radiative heat flow for a reduction and increase, respectively, in heat load. It has also been observed that cattle increase sebum secretion with heat stress, which gives the hair a reflective and protective sheen against solar radiations (Brody, 1956). There is evidence of the existence of a major gene, designated as the *slick hair* gene, which is responsible for producing a very short, sleek hair coat (Olsen et al., 2003). Cattle with slick hair were observed to maintain lower rectal temperatures compared to animals whose coats are more wooly (Olsen et al., 2003). Cattle also go through seasonal variations in coat characteristics. Seasonal changes in hair

cover are influenced by daily photoperiod as well as by ambient temperature, when cattle shed their winter hair coat to better allow for heat exchange. In addition, the rate of shedding is associated with the thermal status of the animal (Webster, 1974). Dowling (1956) found that differences in winter and summer coats altered the core temperature of shorthorn cattle, although the difference was not substantial.

4.1.2. Physiological

Body size also has an impact on adaptation to hot environments. Extra-large skin folds result in a larger surface area to mass ratio and consequently more heat loss per unit of weight. The ears, dewlap, navel flap, and vulva are much larger and more corrugated in the loosely built, heat-tolerant and cold-sensitive Indian cattle than in the compactly built, cold-tolerant and heat-sensitive European cattle. Although there are differences in the surface area and subcutaneous fat layers in heat tolerant and intolerant cattle, other factors are very similar. For example, there are no differences in skin thickness (independent of subcutaneous fat) between Indian and European cattle (Dowling, 1955).

4.1.2.1. Metabolism

The known modes of adaptation of the animal to its thermal environment through physiological means includes metabolism, redirection of blood flow, and changes in evaporation. One of the most researched avenues of adaptation is the reduction in heat production or metabolism. Cattle experience reductions in feed intake (Kibler and Brody, 1951), growth rate (Cartwright, 1955), and milk production (Johnson, 1965) in response to heat stress. When these reductions occur it is termed metabolic acclimation, implying adaptation to a variable, such as environmental temperature. (Mount, 1979). By its nature, metabolic acclimation is a form of adaptation that is dependant on a food supply

and level of nutrition. However, other forms of metabolic adaptation exist. For instance, it is generally accepted that the metabolic rate of heat adapted animals is lower than temperate species (Robertshaw, 1985). For example, as environmental temperature rises, feed consumption by tolerant cattle may begin to decline around 32-35°C, whereas intolerant cattle may decline closer to 26-29°C (Ingram and Mount, 1975). The heat tolerant cattle have a lower metabolic rate and make more efficient use of ingested food (Ingram and Mount, 1975). Their rates of weight gain under hot conditions exceed those of heat intolerant cattle, but are much lower at thermoneutrality. This lower metabolism is a huge advantage under hot conditions. In fact some breeds of tolerant cattle are able to maintain a lower rectal temperature while evaporating 40% less than heat intolerant cattle.

4.1.2.2. Blood flow

A major adaptation to thermal stress is peripheral vasodilation and increased blood flow to accommodate evaporative and convective heat losses (Beede and Collier, 1986), concomitantly reducing blood flow to internal organ systems such as the reproductive tract and ruminant stomachs. The vasomotor response is the cheapest of all thermoregulatory defense reactions. The only energy expenditure is in the form of cardiac work, which constitutes only a small portion of total energy expenditure. Engelhardt and Hales (1977) quantified distribution of capillary blood flow to the muscular and mucosal layers of the rumen, reticulum and omasum of sheep experiencing various thermoregulatory demands. They reported that 7% of cardiac output was to the stomach regions and 95% of blood flow was in the mucosa and while only 5% to the muscle layers at thermoneutrality. During exposure to heat stress (40°C) blood flow decreased in

mucosa of the dorsal rumen by 32%, and was reduced 31% in the reticulum, compared with the thermoneutral environment (18°C). Blood flow to the omasal mucosa tended to increase, while flow to muscle layers were unaffected by heat stress. They also found that heating deep-body thermoreceptors (hypothalamus) lowered blood flow in the mucosa by 17%, and 56% in the muscle, compared with thermoneutral controls. There is some evidence that suggests blood flow to the digestive tract is influenced by the level of feed intake (Lomax and Baird, 1983). Therefore, a reduction in blood flow to the digestive tract during heat stress may be due to the direct effect of ambient temperature or a combination of temperature and reduced in feed intake. There is also some evidence showing that genetically selecting for major physiological defense mechanisms against rising body temperatures, such as reduced feed intake and increased peripheral blood flow combined with a reduction in flow to other tissues, offers little potential advantage for either milk production or growth rate (McDowell, 1982).

Thermal insulation is decreased, particularly by vasodilation and increased blood flow to the skin of the extremities and ears, which have relatively little hair cover and a high surface area to volume ratio. These factors increase heat transfer between animal and environment. Vasodilation under a heavy coat contributes little to heat exchange because the consequent decrease in internal insulation is only a small portion of the total insulation. Blood flow to the periphery increases so that heat loss via conduction and convection is enhanced (Choshniak et al., 1982). Blazquez et al. (1994) reported that increased blood flow to the skin is positively correlated to the sweating rate.

4.1.2.3. Sweating rate

The majority of studies looking at sweating rate over the last 50 years took place under well-controlled conditions in climate chambers. In most of this work, animals were exposed to constant thermal conditions for a few hours to 2 weeks, with or without acclimatization. Although such studies with simplified environments throw light on basic physiology, they cannot anticipate with any accuracy reactions in the field where solar heat load is important and there are diurnal and seasonal cycles of thermal conditions (Schleger and Turner, 1965). The practical significance of differences in sweating rates can only be gained from larger numbers of animals under field conditions. Unfortunately, such conditions contain a lack of environmental control and of the difficulty of interpretation associated with short-term fluctuations in environment making it difficult to obtain precise information. These issues demonstrate the problems in studying the changes in sweating rate during long-term heat exposure.

In an extensive study looking at changes in sweating activity over multiple seasons, Schleger and Turner (1965) found striking differences in sweating rates between summer and autumn-winter periods. These differences were in spite of the fact that respiration rates and rectal temperatures were similar during all seasons. McLean (1963) found during a 7 month experiment that respiration rate, and both skin and rectal temperatures declined over time while sweat rate increased. He attributed this to both age and seasonal effects. Kibler and Yeck (1959) found no difference in sweating of calves raised at 10.0 and 26.6°C when subsequently exposed to a range of environmental conditions. This lack of acclimatization evidence in cattle demonstrates that the seasonal difference in sweating function is more likely associated with the marked seasonal variation in hair growth (Turner and Schledger, 1960) and level of skin activity (Dowling

and Nay, 1960) which is under photoperiodic control (Yeates, 1955). Hayman and Nay (1958) and Nay and Hayman (1963) found that sweat glands of cattle reached a minimum size in summer, so the seasonal difference in sweating competence is not accounted for by gland size. They hypothesized that this is associated with physiological status of the skin, under the influence of endocrine, vascular and nervous factors, varying with the season cycles of follicle activity.

As cattle adapt to chronic thermal stress their energy metabolism or basal metabolic rate decreases, while water and electrolyte metabolism increase (Johnson et al., 1967; McDowell et al., 1968; Collier et al., 1982). These adaptations are reflected in lower concentrations of hormones such as thyroxine (Bianca, 1965; Collier et al., 1982) and growth hormone (Mitra et al., 1972). Although aldosterone concentrations also are lower in chronically heat-stressed cattle it is a reflection of need to increase urinary sodium loss to conserve potassium (Beede and Collier, 1986). Collectively, these results indicate that lowered energy metabolism is a major adaptation in chronic thermal stress. Likewise, increased water and electrolyte metabolism are associated with adaptation to thermal stress as evaporative cooling requirements increase with heat stress (Beede and Collier, 1986).

4.2. Heat tolerance

Heat tolerance in its simplest form is the ability to tolerate ambient temperatures above UCT. For homeotherms, they are often characterized as heat tolerant if they remain comfortable or are able to balance heat production and heat loss at particularly high ambient temperatures (IUPS Thermal Commission, 2001). The ability to describe heat tolerant cattle is very subjective and lacks a true definition. Dowling (1956) stated that

the ability of cattle to withstand a hot environment may be determined by studying the animal's immediate reactions to heat stress as measured by increases in respiration rate and body temperature, or by measuring productivity in terms of reproduction or milk production. While production is the end result and probably the best overall indicator of heat tolerance, it also takes the longest to record. Therefore, most researchers use a measure of body temperature (rectal, abdominal, or ruminal). It would appear, therefore, to be a physiologically reasonable and desirable way of assessing an animal's innate overall capacity to cope successively with a hot environment versus an acquired tolerance (Bianca, 1961). Innate tolerance is determined by factors present in an individual from birth whereas acquired tolerance is something that an animal obtains after being in an environment. Any attempt to discern between the two is faced with difficulties, both fundamental and practical (Bianca, 1961).

5. Differences between *Bos Taurus* and *Bos Indicus* breeds

5.1. Physical differences

While the humped cattle of Indian origin (*Bos indicus* or Zebu cattle) and the generally humpless cattle of Europe and Africa (*Bos taurus*) arose from a common ancestor, these subspecies have experienced separate evolutionary pathways. It is unclear how long these pathways have been separated, but the number generally ranges from 8000 years to several hundred thousand years (Loftus et al., 1994). It has been known for many years that *Bos indicus* breeds are better able to regulate body temperature in response to heat stress than are cattle from *Bos taurus* breeds of European origin (McDowell et al., 1954; Cartwright, 1955; Finch, 1986; Gaughan et al., 1999). However, because these Zebu cattle are thermotolerant, the consequences of exposure to heat stress

for milk and meat productions are much less than for *Bos taurus* cattle (Hansen, 2004). These two subspecies have many physical as well as metabolic and physiological differences.

Most *Bos indicus* cattle such as the Brahmans are intermediate in size among beef breeds. Whereas *Bos taurus* cattle, such as the Angus, are usually larger even at birth. *Bos indicus* cattle are known for having a short, thick, glossy hair coat which reflects much of the sun's rays, adding to its ability to graze in the glaring midday sun without suffering from heat strain. They usually possess dark pigmented skin keeping out the intense rays of the sun, which in excessive amounts will damage deeper tissue layers. They possess an abundance of loose skin which ultimately contributes to its ability to withstand warm weather by increasing the body surface area exposed to cooling. *Bos taurus* cattle have darker and heavier hair coats and tighter skin allowing them to be more cold tolerant.

5.2. Physiological differences

Skin temperature is dependant on color. However, it is a good example of a similarity between these two species in that it increases with heat stress (Ingram and Whittow, 1962). In fact, Allen (1961) reported that *Bos taurus* and *Bos indicus* cattle showed similar responses in skin temperature to the same increases in ambient temperature. This increase in skin temperature also paralleled an increase in sweat rate. Allen (1961) found that the increase in skin temperature was linear with ambient temperature, however differences arose when comparing skin temperature versus sweat rate. *Bos taurus* showed an early and linear rise in sweat rate as skin temperature

increased from 32 to 38°C, whereas *Bos indicus* sweat rate did not increase until the skin temperature reached 35°C.

Direct thermal conductance has also been measured, with Brahman cattle exhibiting the highest rate increase in trunk skin thermal conductance as ambient temperature increased from 25 to 41°C (Finch, 1985). The rate of increase of skin conductance (Watts m⁻² °C⁻¹) was 3.95 for Brahman, 2.33 for Brahman cross, and 2.09 for shorthorn (Finch, 1985). In the same study, mean tissue conductance (Watts m⁻² °C⁻¹) showed the same result with Brahman being the highest and shorthorn the lowest. The author concluded that *Bos indicus* demonstrates an ability to lower heat flow into the body to a far greater extent than *Bos taurus* breeds and sustains this low resistance at high levels of heat stress. This would result in higher levels of forced convection in *Bos indicus* breeds. That being said, there is no explanation for this difference and this experiment was a very short-term exposure.

Studies of hair follicles and apocrine glands in *Bos indicus* and *Bos taurus* breeds suggest that *Bos indicus* cattle have a greater capacity to sweat due to greater densities of sweat glands (Dowling, 1955). However, there is considerable variation across breeds and sweating rates. Allen (1961) found that the differences in maximum sweating rates were not much different between the two species (208 g/m²h *Bos taurus* and 216 g/m²h *Bos indicus*) although there were noticeable differences in between individuals. Similarly, Johnson (1970) found that sweat rates increased significantly for both *Bos taurus* and *Bos indicus* as ambient temperature rose to 45°C. Both showed regional differences, with the shoulder region being the highest and the lumbar being the lowest. Though the species differences were not significantly different, *Bos indicus* animals were consistently higher

at all sampling sites. Gaughan et al. (1999) reported similar findings with Brahman and Hereford steers having very similar sweat rates (Brahman, 171 g/m²h; Hereford, 175 g/m²h) when exposed to a THI > 90 for 10 hours. However, unexpectedly he found that Brahman x Hereford cross steers had a significantly greater sweat rate (221 g/m²h). This is supported by Schleger and Turner (1965) who also found that *Bos indicus* influenced cattle have greater sweat rates than *Bos taurus* cattle exposed to the same conditions. However, others have found that crosses perform somewhere in the middle between the two species. Finch et al. (1982) found that in a natural radiant environment the sweating response was greater for *Bos indicus* (294 g/m²h) compared to *Bos indicus* cross (146 g/m²h) and *Bos taurus* (194 g/m²h) which were not different. Finch et al. (1982) also reported that between animals within breeds, the sweating response was negatively correlated with metabolic rate. This suggests that cattle with high sweating rates may have lower metabolic potential for growth rate.

While there is still controversy about the differences in sweating rates of the two species, it is known that there are differences in the sweat glands themselves. Nay and Hayman (1956) reported differences in the location and density of sweat glands between the two species. They reported that *Bos indicus* cattle had a greater number, as well as larger sweat glands than *Bos taurus*. They also reported that the sweat glands were closer to the skin surface compared to *Bos taurus* cattle. These findings are supported by Carvalho et al. (1995) who found that sweat gland perimeter was greater in *Bos indicus* (540µm) compared to native *Bos taurus* (382µm) and imported *Bos taurus* (497µm). Carvalho et al. (1995) suggested that this difference in sweat gland morphology, rather

than sweat gland perimeter (length of the sweat gland), leads to greater cooling capacity of *Bos indicus*.

It is well recognized that respiratory rate differences exist between *Bos taurus* and *Bos indicus* cattle with increasing ambient temperature. At a THI greater than 90, Gaughan et al. (1999) reported mean respiratory rate of Brahman steers was 104 bpm, which was significantly lower than Hereford (134 bpm), Hereford x Boran (171 bpm), and Hereford x Tuli crosses (166 bpm). Hereford x Brahman cattle was intermediate, with a respiratory rate of 139 bpm. This compares to a rate of 33, 68, 50, 55, and 48 bpm, respectively, at a THI < 77. Differences between *Bos taurus* and *Bos indicus* respiration rate were also reported by Allen (1961) who found that *Bos taurus* cattle had a higher rate than *Bos indicus* cattle at all ambient temperatures from 18 to 41°C. However, the increase in respiration rate was approximately the same until ambient temperature reached above 35°C, after which the *Bos taurus* cattle increased more rapidly. Cross breeds respired at rates similar to *Bos taurus* until an ambient temperature of 32°C was exceeded, when their respiration rate became intermediate to the two breeds. Colditz and Kellaway (1972) examined the respiration rate of Friesian, Brahman, and Brahman X Friesian cattle subjected to 28 days heat stress (38°C) or cool ambient temperatures (17°C). The respiration rate of Friesian and Brahman x Friesian cross cattle at 38°C was twice that of their respective genotypes at 17°C (82 and 70 bpm compared to 34 and 35 bpm, respectively). At both ambient temperatures, the respiration rate of Brahman cattle was lower than the other two genotypes (26 and 37 bpm).

5.3. Growth and Metabolism

The level of production achieved by a particular genotype in harsh environments depends on the contribution and expression of many different traits which may be partitioned into those directly involved with production (e.g., food intake and digestive and metabolic efficiency) measured in the absence of environmental stress, and those involved with adaptation (e.g., low maintenance requirement, heat tolerance, and parasite and disease resistance; Seifert, 1984). Several studies (Frisch, 1981; Vercoe and Frisch, 1982) described growth rate and food intake in the absence of stress as the growth potential of an animal. In the absence of stress, voluntary food intake is closely correlated to growth and is highest in Hereford x Shorthorn (*Bos taurus*), lowest in *Bos indicus* and intermediate in *Bos indicus* x *Bos taurus*. Stress depresses growth rate primarily through the depression of food intake, but also by affecting digestion and metabolism (Vercoe and Frisch, 1982). In stressful environments, animals which are more resistant to stress have higher growth rates, lower mortalities, and are consequently more productive (Hetzel and Seifert, 1986). Frisch and Vercoe (1982) postulated that selection for growth rate under continued stress would lead to an animal with high adaptation but low growth potential, similar to the Brahman. Alternatively, selection under continued low stress would lead to a genotype with high growth potential but low adaptation similar to the *Bos taurus* breeds. *Bos indicus* cattle evolved through natural selection in a stressful environment, including a low plane of nutrition. Because of the low plane of nutrition, selection pressure would have operated against growth potential and in favor of a low maintenance requirement (Frisch and Vercoe, 1982). In the Brahman cattle, growth potential and adaptation therefore appear to have a negative genetic correlation. British cattle, on the other hand, have been selected for growth in a relatively stress-free environment on

relatively high planes of nutrition. Selection pressure for growth potential would therefore be increased, but those for adaptive traits remain unchanged.

6. Variation within *Bos Taurus* Species

The ability to maintain homeothermy under heat stress is a valuable asset for cattle in subtropical and tropical regions of the world. Although variation in heat tolerance among breeds and breed crosses has been studied for many years, efforts have been directed toward comparing *Bos taurus* cattle and *Bos indicus* cattle. Searching for a heat tolerant *Bos taurus* breed is a relatively new idea. Initially, producers were searching for a breed that combines heat tolerance with desirable beef traits, such as high carcass quality and strong maternal traits. It was not until 1977 that the first heat tolerant *Bos taurus* breed was brought to the United States (Dept. Ani. Sci.- Oklahoma state, 2008). This breed was the Senepol, and since 1977 it has experienced widespread growth throughout the United States. Also since then, several other heat tolerant breeds have been found, such as the Romosinuano and Tuli.

6.1. Physical differences

Physically heat tolerant *Bos taurus* breeds look very similar to *Bos indicus* cattle. They are usually possess loose skin and have longer legs and ears than other less heat tolerant breeds. They have a short, thick, glossy hair coat aiding in their heat tolerance. They also usually have a darker pigmented skin (Da Silva et al., 2003) than other breeds. However like the *Bos indicus*, these animals do not have as high of a growth rate as other *Bos taurus* cattle. That being said, in tropical areas during the summer these cattle (e.g. Romosinuano) have been shown to have a greater growth rate than Angus or Hereford

cattle (Chase et al., 1997). They achieve this while maintaining a lower respiration rate and rectal temperature (Chase et al., 1997).

Chase et al. (1997) conducted a two year comparison study of Romosinuano, Senepol, Brahman, Angus, and Hereford heifers. They reported that average daily gain in the winter was greater for Angus and Hereford heifers (temperate *Bos taurus* breeds) than for Romosinuano, Senepol and Brahman heifers. However during the summer, average daily gain of Romosinuano heifers was greater ($P < .05$) than for Angus and Hereford heifers, and similar to Brahman heifers. Under summer conditions, rectal temperature and respiration rates were greater in Angus than in Brahman, Romosinuano, or Senepol heifers. This data confirmed the heat tolerance differences associated with the adapted tropical breeds and also supported the greater average daily gains observed during summer for the tropical breeds compared to the temperate breeds. Though not specifically measured, this data is consistent with the thought that a lower metabolism is the reason for their heat tolerance.

6.2. Heat Tolerance

In another study using similar breeds, Hammond et al. (1996) found that on both the hottest and coolest days of the study, Angus heifers had a significantly faster respiration rate than Romosinuano and Senepol heifers. He reported that on the hottest day of summer, rectal temperature in Angus heifers was greater than the Senepol heifers. However, reciprocal crosses of Hereford and Senepol had rectal temperatures that were similar to that of Senepol. These results again demonstrate the superior heat tolerance of the Senepol and Romosinuano compared to other *Bos taurus* breeds. Furthermore, their results suggest a substantial level of dominance of the Senepol's ability to maintain

constant internal body temperature in a hot environment as measured by rectal temperature and transmit this ability to crosses with a non-adapted breed. In one of the only chamber tests, Spiers et al. (1994) found similar results with an Angus x Romosinuano F1 cross showing superior heat tolerance compared to Angus alone. They reported the superior heat tolerance of the Romosinuano compared to the Angus was due to a greater increase in cutaneous evaporative water loss. However, the F1 cross showed no difference in heat exchange compared to the Angus, suggesting a reduced metabolic rate. In a study by Hernández-Cerón et al. (2004), they found that heat tolerance may start at the embryo. They reported that the embryos from Romosinuanos are more resistant to elevated environmental temperature than embryos from Angus cattle. Their conclusion was that the process of adaptation of *Bos taurus* breeds to hot environments may be the result genetic selection of genes controlling thermotolerance at the cellular level.

CHAPTER II

REGIONAL DIFFERENCES IN SWEAT RATE RESPONSE OF STEERS TO SHORT-TERM HEAT STRESS

Abstract

Six Angus steers (319 ± 8.5 kg) were assigned to one of two groups (hot or cold exposure) of three steers each, and placed into two environmental chambers initially maintained at 16.5 – 18.8°C air temperature (T_a). Cold chamber T_a was lowered to 8.4°C , while T_a within the hot chamber was increased to 32.7°C over 24 hours. Measurements included respiration rate, and both air and body (i.e., rectal and skin) temperatures. Skin temperature was measured at shoulder and rump locations, with determination of sweat rate using a calibrated moisture sensor. Rectal temperature did not change in cold or hot rooms. However, respiration rate nearly doubled in the heat ($P < 0.05$), increasing at a T_a above 24°C . Skin temperatures at the two locations were highly correlated ($P < 0.05$) with each other and with T_a . In contrast, sweat rate showed differences at rump and shoulder sites. Sweat rate of the rump exhibited only a small increase with T_a . However, sweat rate at the shoulder increased more than 4-fold with increasing T_a . Increased sweat rate in this region is supported by an earlier report of a higher density of sweat glands in the shoulder compared to rump regions. Sweat rate was correlated with several thermal measurements to determine the best predictor. Fourth-order polynomial expressions of short-term rectal and skin temperature responses to hot and cold exposures produced r values of 0.60, 0.84, and 0.98, respectively. These results suggest that thermal inputs other than just rectal or skin temperature drive the sweat response in cattle.

Key Words: Cattle, Sweat Rate, Heat, Stress, Acute

Introduction

It has been known since 1835 that mammals have sweat glands, when Gurlt described them as small oval sacs (Kölliker and Busk, 1853). However, it was believed until the late 1950s that bovine sweat glands were poorly functional. Worstell and Brody (1953) concluded that cattle, unlike man, do not sweat. Dowling (1958) was the first to clearly demonstrate that sweating in cattle is important for thermoregulation. It was also established in the 1950s that bovine sweat glands are apocrine and associated with hair follicles (Findlay and Yang, 1950; Dowling, 1955; Nay and Hayman, 1956). Further research has shown there are regional anatomical differences in sweat gland density, with fewer in rump versus shoulder regions of dairy cattle (Findlay and Yang, 1950). The thermal inputs driving the sweating response is controversial. Several experiments suggest that T_{skin} is the major input driving sweat rate (Berman, 1971; Whittow, 1962); while others note that core body temperature is the driver (Finch et al., 1982; Schleger and Turner., 1965). This experiment addressed three questions: Are there regional differences in sweat rate? How does the thermal environment affect sweat rate? What is the best thermal predictor or determinant of short-term sweat rate (air, skin, or rectal temperature)?

Materials and Methods

Animals

Six Angus crossbred steers (319 ± 8 kg BW, 8 months old, BCS 4-5) were obtained from the University of Missouri and housed in the Brody Environmental Center at the same university. Animals were maintained at the University of Missouri Beef Farm

during winter until December when they were moved to the chambers. Animals were divided at random into cold ($n = 3$) and hot ($n = 3$) temperature exposure groups and individually maintained in stanchions (Minimum Area = 1.2 x 3.1 M), with water and feed available *ad libitum* (MFA Cattle Charge, Columbia, MO), and.

General Procedure

Steers were placed in two chambers on Day 1 and maintained at 16.5 – 18.8°C air temperature (T_a) (~61 - 64 THI) for one day of thermoneutral adaptation on a 12 hour light: dark schedule (**Period 1**). Relative humidity was maintained under 50% during for the entire experiment, to reduce the effect of water vapor pressure and focus on changes in T_a . Beginning at 1300 on Day 2 (**Period 2**), T_a was shifted to 8.4 (~ 50 THI) and 32.7°C (~82 THI) (**Period 3**) for cold and hot chambers, respectively. These T_a were achieved at approximately 2400 on Day 2 and maintained at a stable level through the 1300 measurement on Day 3 (**Period 4**). This measurement was followed by a rapid return to thermoneutrality (~17.0 – 20.5°C; ~ 61 – 66 THI) and measurement at 1600 on the same day (**Period 5**). The largest rate of increase in T_a of both rooms was 1.7°C per hour. Thermoregulatory measurements were taken during the five different periods (Fig. 2.1). Shoulder and rump skin regions were shaved before the start of the experiment to allow for skin temperature (T_{skin}) and sweat rate measurements. It was essential that measurements were made at the skin surface in the absence of hair, since hair is hygroscopic and would trap moisture at the skin surface to impede sweating. Skin temperature was measured over a 1 minute period using an infrared thermometer (Model C-1600M, Linear Laboratories, Fremont, CA). Rectal temperature (T_{re}) was measured

with a thermistor thermometer (Cole-Parmer Instruments, Chicago IL). Determinations of respiration rate (respirations per minute, RPM) were made by counting flank movement over a one minute interval. Air temperature was measured by reading a calibrated thermometer that was placed in the room approximately 0.3 M above the center animal in each room. Baseline measurements of all thermoregulatory parameters were made at thermoneutrality prior to the change in T_a . This was followed by similar measurements at selected periods during thermal stress.

Sweat rate was determined using a calibrated, digital moisture sensor (Vapometer; Delfin Technologies Ltd, Finland) that has been used to determine transepidermal water loss of humans and cattle (Nuutinen et al. 2003; Gebremedhin et al. 2007). Recent studies have used the same type of device to measure moisture loss in a range of situations and environments (Nuutinen et al. 2003). Its response time is usually less than 15 seconds, with minor accumulation of water vapor within the closed-cell sensory capsule.

Statistical Analysis

Data was analyzed using two-way repeated-measures ANOVA procedure and standard least squares model fit (JMP[®]; SAS Institute, Inc., Cary, NC). Components of the statistical model included room, period, and room by period interactions. When ANOVA revealed a significant difference ($P \leq 0.05$) in least squares means, a Tukey-Kramer multiple comparisons test (Steel and Torrie, 1980) was performed to determine both between- and within-treatment effects. Statements of significance always refer to $P \leq 0.05$ when not indicated otherwise in parentheses. Multivariable correlation analysis was evaluated using the Fit Line and Fit Polynomial commands (JMP[®]; SAS Institute,

Inc., Cary, NC) estimated by least squares regression to determine linear and quadratic relationships between selected variables.

Results

Rectal temperature (Fig. 2.2; 38.7 versus $39.0 \pm 0.1^\circ\text{C}$) and respiration rate (Fig. 2.3; 65 versus 78 ± 6.2 RPM) were not different between test groups during adjustment to the thermoneutral condition (Period 1; $P>0.08$). Also, a comparison of temperatures across shoulder and rump skin sites for all sample times showed no site differences ($P>0.86$), with site averages for the study being 33.86°C (Rump) and 33.81°C (Shoulder). Therefore, the values for these sites were averaged to derive a more reliable estimate of mean T_{skin} . Hot and cold rooms did not differ for T_{skin} during Period 1 (Fig. 2.4; 33.5 versus $35.6 \pm 0.5^\circ\text{C}$). Likewise, sweat rates at the two skin sites were not different at thermoneutrality (Shoulder: 40.0 versus 46.0 ± 8.0 g/m²h; Rump: 43 versus 52.6 ± 3.0 g/m²h). These results show that there were no group differences in determinants of thermal status prior to the change in T_a .

Cold exposure during Period 2 (i.e., transition period) did not produce a change ($P>0.42$) in T_{re} (Fig. 2.2; 38.7 versus 38.9°C). However, there were significant decreases in T_{skin} (Fig. 2.4) by 2°C and respiration rate by 20 RPM (Fig. 2.3) from thermoneutral level. Likewise, shoulder and rump sweat rates exhibited a significant reduction (20 g/m²h) from Periods 1 to 2.

Rapid heat exposure during Period 2 also did not produce a significant increase in T_{re} (Fig. 2.2; 38.9 versus 38.6°C). Skin temperature increased in the heat (35.6 versus 36.9°C ; $P<0.001$) and was the earliest indicator to become significantly different

($P < 0.05$) during Period 2. However, unlike during the cold challenge, respiration rate (78 to 82 RPM; Fig. 2.3) and sweat rate (46.0 to 46.8 g/m²h) did not change ($P > 0.10$) during the transition phase.

As expected, steady-state exposure to heat and cold conditions (i.e., Periods 3 and 4) produced more reliable changes in most indicators of thermal status. Rectal temperature, which is the more traditional indicator, remained stable during these periods in the cold (38.7 and 38.5°C, respectively; Fig. 2.2). In contrast, respiration rate (Fig 2.3; 36 and 34 RPM, respectively) and T_{skin} (Fig 2.4; 29.6 and 29.2°C, respectively) continued to decrease and were significantly different from Period 1. Shoulder and rump sweat rates remained low during Periods 3 and 4 in the cold, only being different from Periods 1 and 5.

Mean rectal temperature in the hot exposed group was different from the thermoneutral level (38.9 to 39.1°C; Period 1 vs. Period 3) after 23 hours exposure (Fig. 2.2; $P < 0.05$). Respiration rate in Period 3 increased by nearly 50 RPM (Fig. 2.3; $P < 0.001$), and was maintained at this level through Period 4. Skin temperature remained above thermoneutral level during Periods 3 (Fig. 2.4; 35.6 to 37.9°C) and 4 (Fig. 2.4; 37.9°C). Sweat rates of shoulder and rump sites were very different ($P < 0.01$), with the shoulder site increasing more than 4-fold above the level at 27°C (46.8 to 224.8 g/m²h) and rump sweat rate only showing a slight increase (51.4 to 59.0 g/m²h). Like other parameters, shoulder sweat rate peaked during Periods 3 and 4 (224.8 and 153.6 g/m²h, respectively; $P < 0.001$). Rump sweat rate showed only a slight increase, from previous periods ($P > 0.25$).

Nearly all measured values in the cold room during Period 5 (return to thermoneutrality) were similar to those from Period 1 at thermoneutrality. Rump sweat rate, being the exception, was lower from Period 1 (27.3 versus 42.9 g/m²h, $P<0.05$), but not different during the other periods. Similarly to the cold room, the return to thermoneutrality from heat stress in the hot room resulted in a re-establishment of thermoneutral level for most variables. Skin temperature however, was lower during Period 5 compared to Period 1 (Fig. 2.4; 32.7 versus 35.6°C; $P<0.05$). As seen during the cold exposure, rump sweat rate during Period 5 following heat stress was below Period 1 level (52.6 versus 33.7 g/m²h; $P<0.01$).

All measured parameters were evaluated to determine correlation coefficients and predictors of acute heat and cold stress. Air temperature was highly correlated with most parameters (r from 0.60 to 0.98). Skin temperature was linearly correlated with T_a ($r = 0.94$; $P<0.001$). Respiration rate also revealed a high correlation with T_a , but showed a quadratic relation rather than linear (Fig. 2.5a; $r = 0.90$ versus 0.93; $P<0.001$). Respiration rate also showed a good correlation with T_{skin} (Fig. 2.7a; $r = 0.93$; $P<0.001$). However, unlike T_{skin} and respiration rate, T_{re} showed a much poorer relationship to T_a (Fig. 2.5c; $r = 0.60$; $P<0.01$). Rectal temperature had the lowest correlation with T_a for all variables, including T_{skin} (Fig. 2.6c; $r = 0.50$; $P<0.01$) and respiration rate (Fig. 2.6a; $r = 0.60$; $P<0.01$), to suggest that it is not a good indicator of acute heat or cold stress.

Finally, thermoregulatory effectors of heat loss were evaluated to determine potential drivers of sudomotor activity. Consistent with the above results, T_{re} showed the lowest correlation with sweat rate at both sites (Fig. 2.6b; Shoulder, $r = 0.61$; $P<0.001$; Rump, $r = 0.52$; $P<0.01$). Skin temperature on the other hand was highly correlated with

shoulder ($r = 0.86$; $P < 0.001$) and rump sweat rates (Fig. 2.7b; $r = 0.82$; $P < 0.001$). Respiration rate was also highly correlated with shoulder ($r = 0.93$; $P < 0.001$) and rump ($r = 0.82$; $P < 0.001$) sweating rates. Both respiration rate and T_{skin} yielded high correlations, suggesting they may be good indicators or potential drivers of sweating activity. However, the superior correlation coefficient was for shoulder sweat rate versus T_a (Fig. 2.5b; $r = 0.98$; $P < 0.001$). The best fit relationship for shoulder sweat rate with T_a was a fourth-order polynomial relationship. Rump sweat rate, which also exhibited a high correlation (Fig. 2.5b; $r = 0.82$; $P < 0.001$), showed more of a linear increase with T_a .

Discussion

Rectal temperature is often used as the indicator of thermal status, but is also the response with the greatest lag time. This was verified in the present study which showed little change in this parameter in response to short-term thermal stress. This lag in rectal temperature response behind T_a is seen in acute heat stress trials (Lefcourt and Adams, 1996) and is attributed to the effectiveness of physiological heat dissipaters (e.g., respiratory and cutaneous evaporations). Likewise, the size of the cattle in this study provides thermal inertia which would predictably slow both the increase and decrease in body temperature and, in effect, result in little change in core temperature. This characteristic of large ungulates has been reported by others (Cain et al. 2006; Verwoerd et al. 2006).

Skin temperatures recorded in the present study changed rapidly with T_a . In both the cold and hot rooms, T_{skin} was linearly related to T_a . This is expected since the monitored sites were located on the trunk region of the animal. The animal's trunk region

is not as sensitive to vasomotor activity as the appendages (Ames et al., 1970). This has been demonstrated by using skin temperature change alone to identify vasomotion (Slee, 1968). In this cold stress study using sheep, it was reported that T_{skin} at the extremities decreased at the rate of 1°C per degree centigrade decrease in T_{a} , suggesting vasoconstriction. However, T_{skin} at the trunk only showed a marginal decrease. Slee (1968) suggested that T_{skin} must increase or decrease at the rate of 0.4°C per degree centigrade change in T_{a} to signify a vasomotor activity, which was not observed in the current study. Unlike recovering from cold exposure in the present study, when T_{skin} returned to thermoneutral level, recovery from heat stress decreased T_{skin} below thermoneutrality. This could be due either to variations in T_{a} or overcompensation of vasomotor activity due to a shift in the zone of thermoneutrality (Settivari et al., 2007). Romanovsky et al. (2002) noted in a review that exposure of a variety of animals to a low T_{a} shifted the thermoneutral, upper critical and lower critical zones to lower levels. Therefore making what is normally a thermoneutral T_{a} into a relatively hot T_{a} . The opposite response would be expected following heat stress, with the previously thermoneutral T_{a} becoming a cold T_{a} . This would cause increased vasoconstriction at this T_{a} and result in a lower skin temperature.

Respiration rate rose and fell with T_{a} in the present study in a manner similar to that seen in acute heat or cold stress experiments, respectively (Brown-Brandl et al., 2003). This variable has been used as a sensitive indicator of heat load in animals during hot weather (Hahn, 1999), with the increase occurring prior to changes in body temperature, feed intake, etc. Likewise, McDowell (1972) stated that increased respiration rate is the first outward indication that cattle are responding to increased

thermal load. Respiration rate in our study increased before T_a reached 25°C; whereas sweating rate, a less sensitive indicator responded only to T_a above 25°C. McLean (1963) also found this, stating that at 15°C, the rate of moisture vaporization for all regions was around 10 g/m²h, with no increase in vaporization until T_a was above 25°C. McDowell et al. (1954) also found that sweat glands of cattle increase sweat production at approximately 25°C which is consistent with our results. These results have important implications for beef and dairy producers, showing that technological devices such as thermometers or the Vapometer, in this case, are not necessary to determine heat strain in cattle.

Evaluation and interpretation of sweat rate measured using a closed-cell device, such as the Vapometer, assumes that this is the appropriate rate for the entire animal surface in the natural environment. However, it is known that different techniques will generate different values for sweat rate. For example, another approach to measuring sweat rate is to use an open-flow capsule with a constant flow of air over the skin. This technique assumes that air movement is constant over the entire animal, like the closed-cell approach, and the rate of loss is constant over the entire animal surface. Both systems were recently evaluated by Gebremedhin et al. (2007). As expected, the latter approach yielded a higher absolute sweat rate compared to the closed-cell technique. The higher amount is likely due to the passage of dry air over the skin and continuous removal of water from the skin surface. Although the closed-cell device rapidly samples the water vapor (i.e., < 1 minute) to minimize any accumulation of moisture, it is not constantly sampling from a dry surface. Fortunately, both systems show a similar pattern of change

in sweat rate (Gebremedhin et al., 2007). It remains to be determined which values represent the “true” sweat rate from the skin.

There is controversy in the literature concerning the mechanisms of sweating that include the driving force and functionality. It is known that there are regional differences in the number of sweat glands; the shoulder region possesses a greater number than the rump region (Fig. 2.8; Findlay and Yang, 1950; McLean, 1963). Though not specifically evaluated in Angus, it is generally accepted that all cattle possess these regional differences in sweat gland densities (Dowling, 1955; McDowell et al., 1955; Kibler and Yeck, 1959). Similar to the results shown in this experiment, McLean (1963) found that the shoulder regions of Ayrshire cattle have a greater sweat rate compared to the rump region. The mechanism or controller driving sweat rate is poorly understood. Researchers (Berman, 1971; Whittow, 1962; McLean, 1963; Schleger and Turner, 1965) have tried to correlate different measurements (ie. respiration rate, T_{re} and T_{skin} , T_a) to find the best predictor of sweat rate. The results of the present experiment show that T_a is the best predictor under short-term conditions. Others have found that T_{skin} is a reliable predictor of sweat rate in cattle (Berman, 1971; Whittow, 1962; McLean, 1963). Berman (1971), in a field study, reported that over a wide range of T_a (8°C to 40°C), the relationship of sweat rate to mean skin temperature was linear, and this relationship remained in effect across season. McLean (1963) noted that exposure of cattle to a constant T_a of 38°C for three days resulted in a stepwise increase in vaporization rate with an increase in T_{skin} . Each sharp increase in vaporization rate coincided with a sharp increase in T_{skin} to support the importance of this thermal input in determining this response. Similarly, Whittow (1962) stated that since the T_{skin} of the trunk does not change very much at

different T_a , it is likely that changes in skin temperatures of the extremities, which undergo considerable temperature change, may influence sweat gland activity in those specific areas. Finch et al. (1982) found that under extreme heat stress, core body temperature provided the best correlation with sweat rate of different breeds. Rectal temperature may, in fact, be the better predictor in cattle following heat adaptation. This phenomenon has been seen in heat adapted humans (Colin and Houdas, 1965). Schleger and Turner (1965) found that during periods of low heat stress in cattle, T_{skin} and coat score (a subjective assessment - with scores ranging from 1 to 7; 1 represents an extremely short coat and 7 is a very wooly coat; Turner and Schleger, 1960) were highly correlated to sweat rate. However, T_{re} and coat score had the greater correlation during heat stress. The present study suggests that T_a is the better predictor of sweat activity under short-term conditions (i.e., less than 24 hours). Murray (1966) found that major differences between sweat rates of shaded and unshaded steers were unrelated to T_{re} or T_{skin} . He hypothesized that T_a and solar radiation were the best predictors of sweat rate. In fact, under field conditions, Murry (1966) reported that cutaneous evaporation rates were twice those obtained during a climate laboratory test even though animals showed lower T_{re} , respiratory rate, and T_{skin} . He also noted that evaporation rates of Hereford and Hereford cross calves could be reduced by up to 60% by protecting them from direct sunshine. The present study demonstrates that while there is a good correlation for respiration rate and T_{skin} with sweat rates, the best predictor is T_a during heat stress. Although T_a had the highest correlation with sweat rate, it is not directly responsible for this activity since it must be “translated” at a receptor level to produce the noted effect.

This study could not identify the direct input or, more realistically, combinations of inputs that collectively drive the sweat response.

Figures and Legends

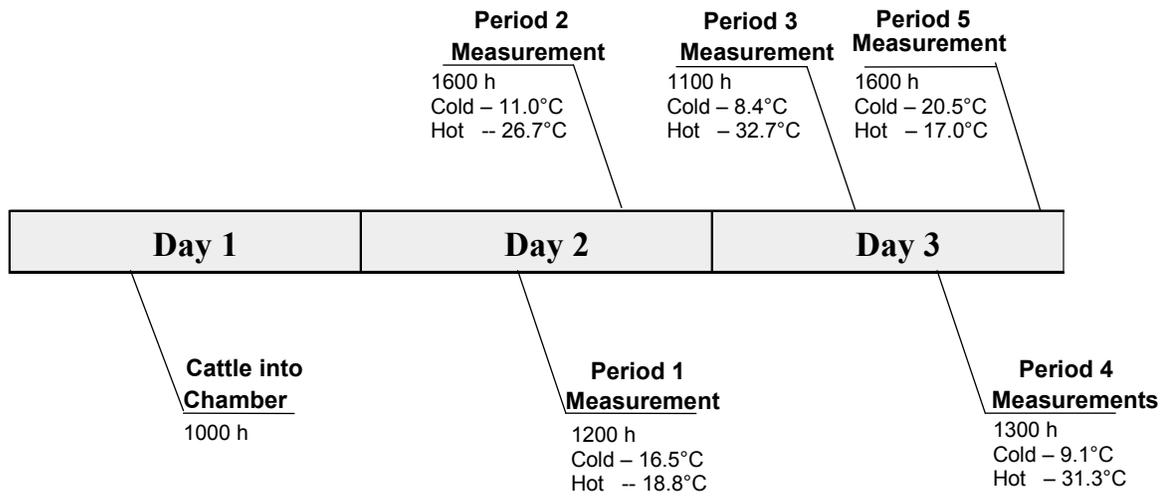


Figure 2.1. Timeline of measurements. Cold - refers to cold chamber; Hot - refers to hot chamber

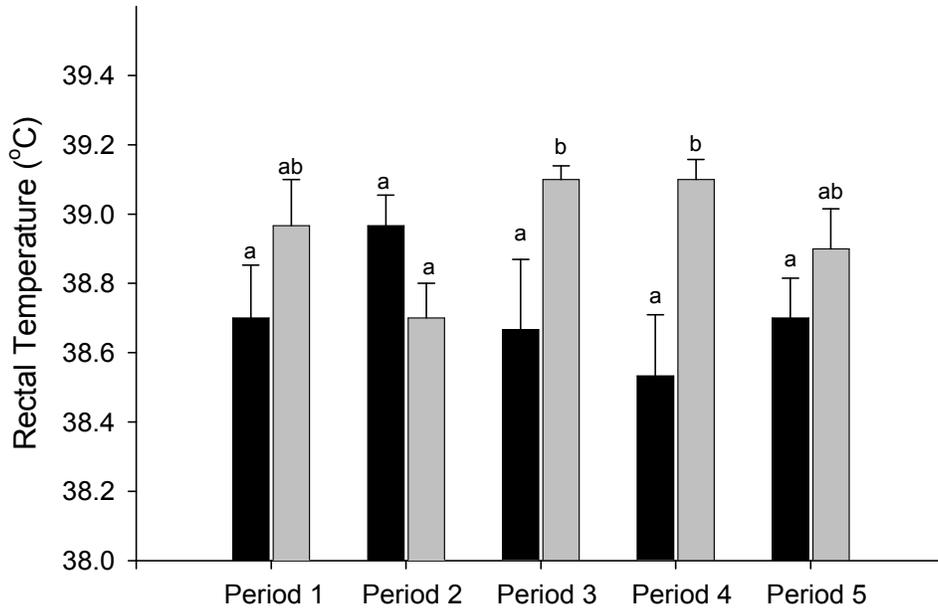


Figure 2.2 Mean rectal temperature (°C) for both hot and cold rooms as a function of period measurement. ■ Cold Room ■ Hot Room. Error bars represent ± 1 standard deviation. ^{a,b,c} within a room with different superscripts are different ($P < .05$). ^x within a period with different superscripts indicate a different thermal group response ($P < .05$).

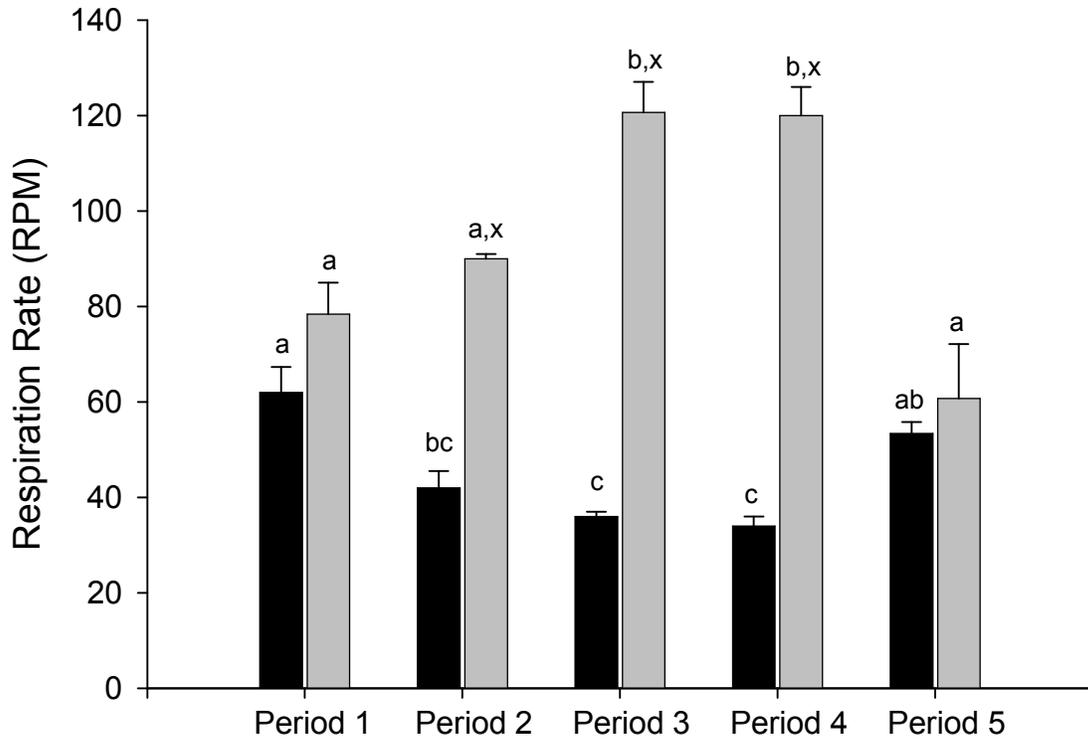


Figure 2.3. Mean respiration rate (breaths per minute) for both hot and cold rooms as a function of period measurement. ■ Cold Room ■ Hot Room. Error bars represent ± 1 standard deviation. ^{a,b,c} within a room with different superscripts are different ($P < .05$). There were no significant differences within a period across thermal groups

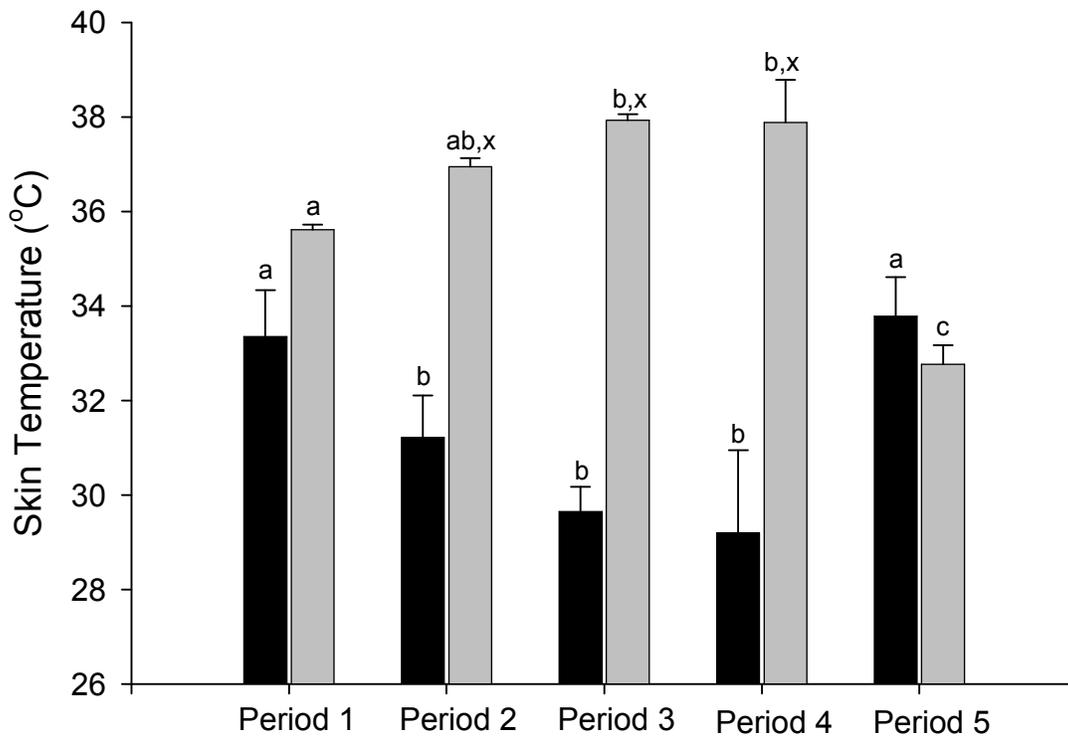


Figure 2.4. Mean skin temperature (°C) for both hot and cold rooms as a function of period measurement. ■ Cold Room ■ Hot Room. Error bars represent ± 1 standard deviation. ^{a,b,c} within a room with different superscripts are different ($P < .05$). ^x within a period with different superscripts indicate a different thermal group response ($P < .05$).

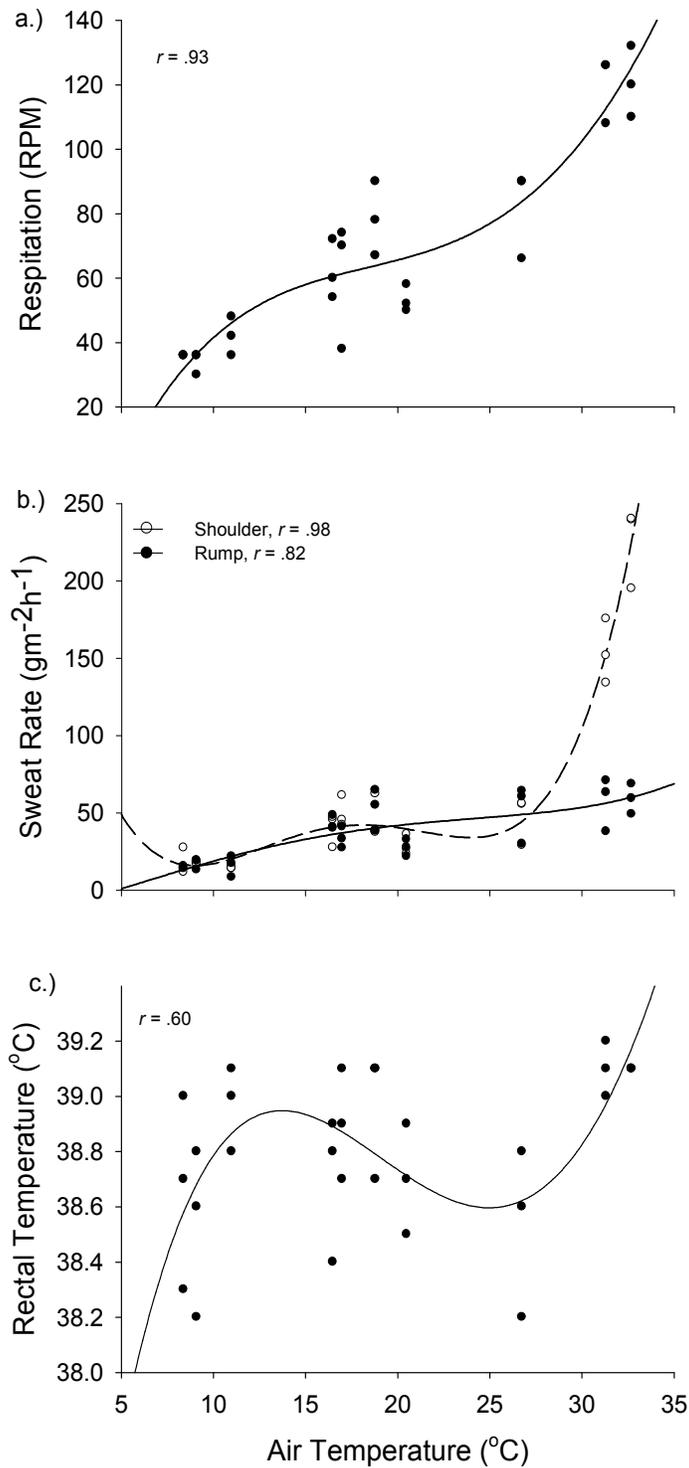


Figure 2.5. a.) Respiration rate (RPM) plotted as a function of air temperature ($^{\circ}\text{C}$). — best fit line; b.) Sweat rate ($\text{g}/\text{m}^2\text{h}$) plotted as a function of skin temperature ($^{\circ}\text{C}$). \circ Shoulder skin site \bullet Rump skin site. ---- Shoulder best fit line — Rump best fit line; c.) Rectal temperature ($^{\circ}\text{C}$) plotted as a function of air temperature ($^{\circ}\text{C}$). — best fit line

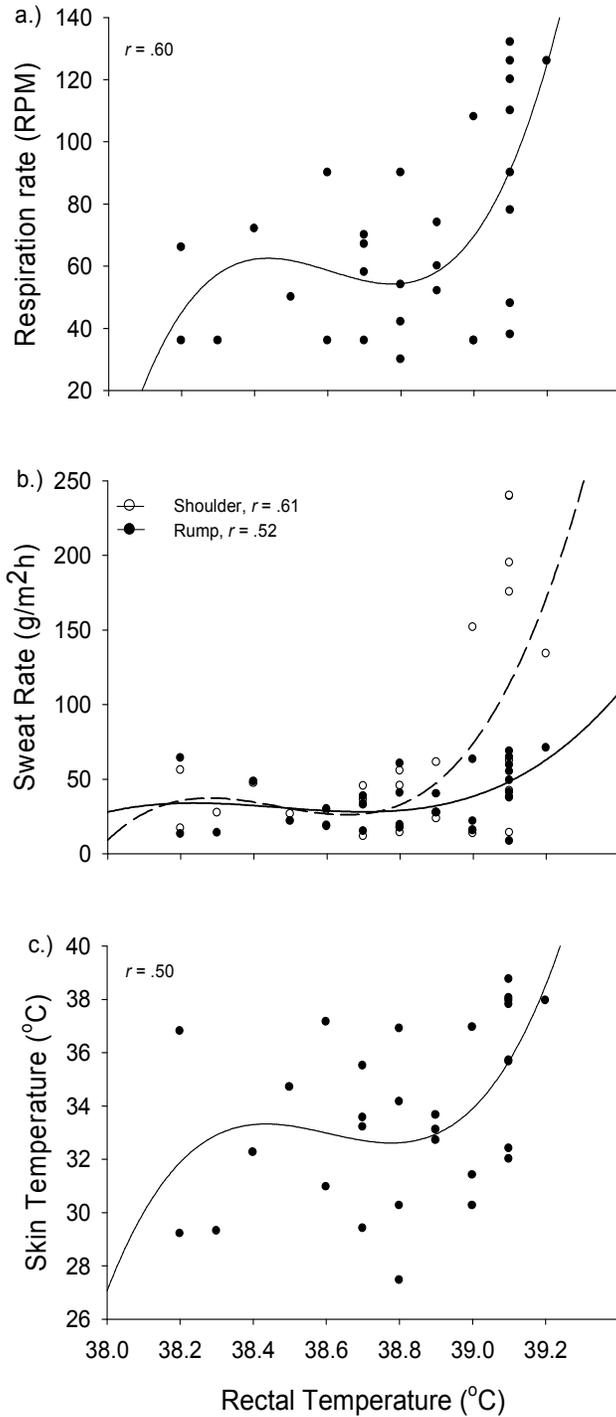


Figure 2.6. a.) Respiration rate (RPM) plotted as a function of rectal temperature (°C). — best fit line; b.) Sweat rate (g/m²h) plotted as a function of rectal temperature (°C). ○ Shoulder skin site ● Rump skin site. - - - Shoulder best fit line — Rump best fit line; c.) Skin temperature (°C) plotted as a function of rectal temperature (°C). — best fit line.

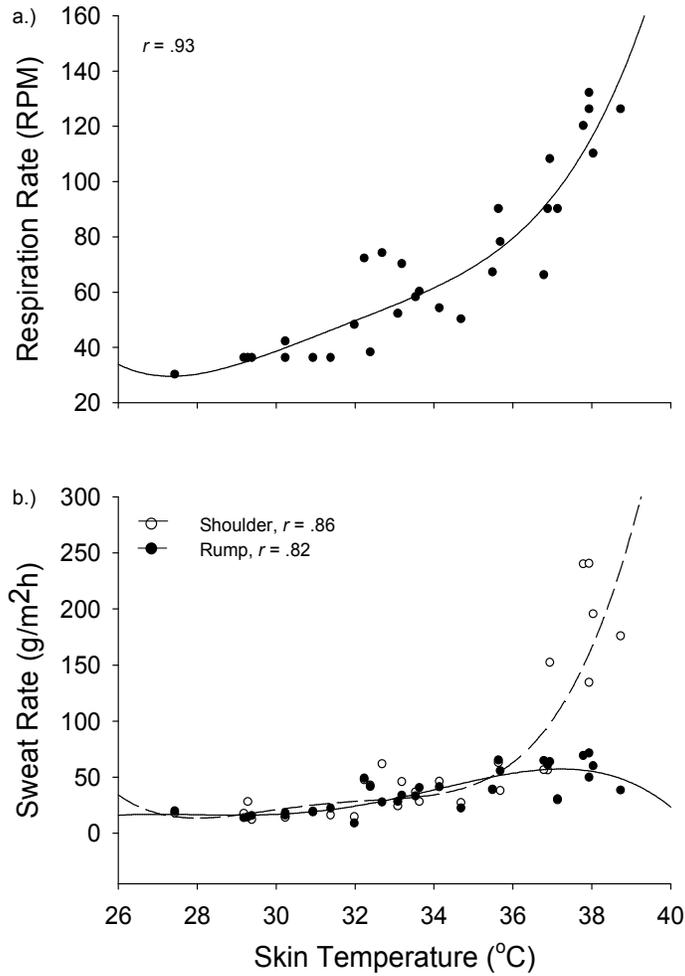


Figure 2.7. a.) Respiration rate plotted as a function of skin temperature. — best fit line; b.) Sweat rate (g/m²h) plotted as a function of skin temperature (°C). ○ Shoulder sweat rate; ● Rump sweat rate; - - - Shoulder best fit line; — Rump best fit line.

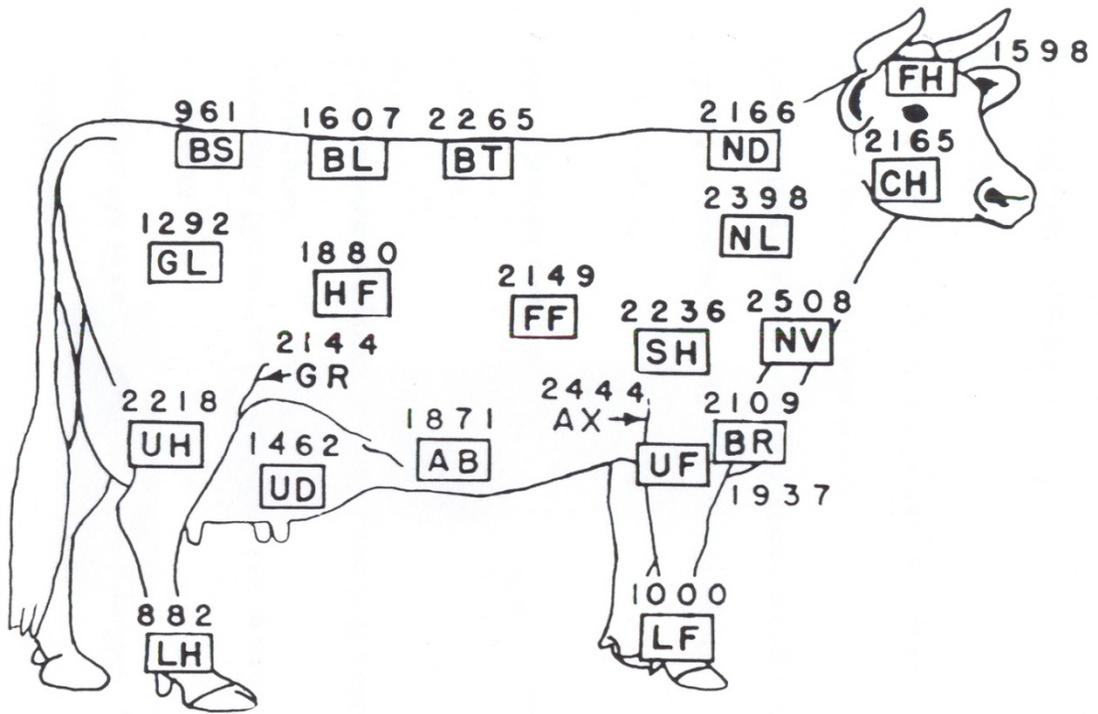


Figure 2.8. Regional differences in sweat gland numbers (see Findlay and Yang, 1950).

Variables	Regression	Correlation Coefficient
Shoulder SR vs T_a	Linear	.82
Shoulder SR vs T_a	Quadratic	.91
Shoulder SR vs T_a	Cubic	.96
Shoulder SR vs T_a	Quartic	.98
Shoulder SR vs T_{shoulder}	Linear	.70
Shoulder SR vs T_{shoulder}	Quadratic	.80
Shoulder SR vs T_{shoulder}	Cubic	.84
Shoulder SR vs T_{shoulder}	Quartic	.85
Rump SR vs T_a	Linear	.79
Rump SR vs T_a	Quadratic	.81
Rump SR vs T_a	Cubic	.82
Rump SR vs T_a	Quartic	.82
Rump SR vs T_{rump}	Linear	.78
Rump SR vs T_{rump}	Quadratic	.78
Rump SR vs T_{rump}	Cubic	.81
Rump SR vs T_{rump}	Quartic	.81
Shoulder SR vs Rump & Shoulder	Multiple Linear Regression	.83
Shoulder SR vs T_a , T_{shoulder} , and T_{re}	Multiple Linear Regression	.86

Table 2.1. Best fit relationship of sweating rates (SR) to air (T_a), skin (T_{shoulder} , T_{rump}), and rectal (T_{re}) temperatures.

CHAPTER III

EVALUATION OF PHYSIOLOGICAL DIFFERENCES IN HEAT TOLERANT AND HEAT SUSCEPTIBLE *BOS TAURUS* CATTLE DURING CONTROLLED HEAT CHALLENGE

Abstract

Two *Bos taurus* breeds with known differences in heat tolerance were tested under controlled conditions to evaluate heat tolerance. Romosinuano (**RO**) is a tropically adapted breed. Nine Angus (304 ± 7 Kg BW; **AG**) and nine RO (285 ± 7.5 Kg BW) steers from USDA-ARS, Brooksville, Florida were transported to the Brody Environmental Center at the University of Missouri. Steers were housed for 14 days at thermoneutrality (21°C ; **TN**) before 14 days of cyclic heat stress (**HS**; 26°C night; 36°C day). Rectal temperature and respiration rate were measured six times daily. Sweat rates at shaved sites were recorded on specific days. Blood samples were taken once a week. The RO maintained a lower respiration rate ($\Delta 20$ bpm), sweat rate ($\Delta 6$ g/m²h), and rectal temperature ($\Delta 0.5^{\circ}\text{C}$) than AG throughout TN. Both breeds increased sweat rate, respiration rate, and rectal temperature during HS, with AG retaining the higher levels. There were breed differences for serum prolactin, leptin, creatinine, and cholesterol, with AG being higher than RO. Serum leptin increased for both breeds with HS. Although there were no breed differences at TN, AG steers exhibited HS-induced increases in prolactin, creatinine, and cholesterol. However, these measures for RO were unaffected by HS. The present study has identified additional physiological and endocrine markers that may aid in the identification of *Bos taurus* sensitivity to heat.

Key Words: cattle, heat tolerance, physiological markers

Introduction

Development of a breed of cattle that can tolerate heat stress and maintain productivity has been a long-term goal of researchers and cattle breeders. Historically, most research in this area has emphasized comparisons of heat tolerant *Bos indicus* cattle (e.g., Brahman) versus heat intolerant *Bos taurus* cattle (Brody, 1956; Gaughan et al., 1999). Comparing the two is difficult due to the many physical and genetic differences.

Current interest has shifted toward using breeds of *Bos taurus* cattle from tropical climates that might be both heat tolerant and superior to *Bos indicus* cattle in terms of reproduction, growth, and carcass quality (Spiers et al., 1994). These breeds include Romosinuano, Senepol, and Tuli. The Romosinuano breed (RO) is a tropically adapted, criollo beef breed that is native to Colombia, S.A. (Chase et al., 1997). Previous research suggests that RO exhibits heat tolerance, as well as good growth and high fertility (Vogt et al., 1991). Likewise, they are noted for longevity, docile temperament, and good combining ability with *Bos indicus* (Elzo et al., 1998). This breed is currently found in Brazil, Costa Rica, United States, and Venezuela (Elzo et al., 1998).

There have been few studies to compare the thermoregulatory abilities of RO and heat sensitive cattle under controlled environmental conditions (Vogt et al., 1991), with most relying on field comparisons (Hammond et al. 1996). Spiers et al. (1994) performed one of the only environmentally-controlled experiments using RO cattle. They were able to demonstrate the RO's superior heat tolerance in a relatively short-term experiment using animals raised in Missouri. Animals in that experiment were subjected to a constant 32.2°C for 7 days. The purpose of this study was to evaluate the thermoregulatory abilities of heat tolerant (Romosinuano) and heat sensitive (Angus) *Bos*

taurus breeds during exposure to a longer heat stress period. It was expected that there would be a better understanding of the RO's heat loss mechanisms by extending the length of heat stress to 14 days and cycling the air temperature. Our goal was to isolate the effect of the environment and concentrate on breed differences by obtaining animals raised in the same region of the United States (i.e., Florida). By using a controlled heat challenge and measuring thermal status and thermoregulatory heat loss mechanisms, it would be possible to identify many of the heat exchange avenues that results in superior heat tolerance for Romosinuano cattle.

Materials and Methods

Animals

Nine Angus (304 ± 7.0 Kg BW; **AG**) and nine Romosinuano steers (285 ± 7.5 Kg BW; **RO**) were obtained from the Subtropical Agricultural Research Station in Brooksville, Florida. Romosinuano steers were originally imported as embryos from a herd at the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) in Turrialba, Costa Rica. (Romosinuanos were imported as embryos and were born in 1991, 1993 (Costa Rican importation) and 1997 (Venezuelan importation). The Angus herd was put together in 1950 from Angus cattle at state research facilities). Embryos were transferred into recipient cows forming the present day herd in Brooksville. Animals in the current study were shipped to Oklahoma before being brought to the University of Missouri in late January. Steers were housed at the University of Missouri South Farm for training prior to entering the Brody Environmental Center at The University of Missouri. Steers were randomly divided into 3 rooms of the Center, with 3 individuals from each breed in a

room and maintained in individual stanchions. Steers were fed a high-concentrate diet (Table 3.1; 39% each of corn and soybean hulls, 20% dried corn distiller's grains, and 2% mineral supplement; as-fed basis) at 1.6% of BW/d, with water available *ad libitum*.

General Procedure

Steers were housed for 14 d at thermoneutrality ($T_a = 21^\circ\text{C}$; TN) before initiation of heat stress. Heat stress (HS) consisted of daily cyclic T_a (26°C night T_a : 36°C day T_a) for 14 days (Fig. 3.1). Environmental conditions were continuously measured using "Hobo" data loggers (Onset, Bourne, MA) to record T_a and %RH every 10 minutes. Measurements including respiration rate, T_{skin} , and T_{re} were taken six times daily (0600, 1100, 1300, 1600, 1900, and 2100). Determinations of respiration rate were made by counting flank movement over a one minute interval. Skin temperature was measured using an infrared thermometer (Model C-1600M, Linear Laboratories, Fremont, CA). Rectal temperature was measured with a thermistor probe (thermistor thermometer; Cole-Parmer Instruments, Chicago IL). Sweat rates were recorded on specific days throughout the study on shaved shoulder and rump sites, and was determined using a calibrated, digital moisture sensor (Vapometer; Delfin Technologies Ltd, Finland) that determined transepidermal water loss. Other recent studies have used the same type of device to measure moisture loss in a range of situations and environments (Nuutinen et al. 2003).

Blood samples

Blood samples were collected during thermoneutral and heat exposure periods via the jugular vein. They were centrifuged immediately to obtain the serum, and frozen (-20°C) for later use. Serum analyses used standard procedures. Most of these measurements were components of a larger biochemical profile produced by the Veterinary Medical

Diagnostic Laboratory, University of Missouri-Columbia using an auto-analyzer (Olympus AV400; Olympus America, Inc., Melville, NY). Plasma leptin concentrations were determined by a highly sensitive ovine leptin RIA validated for bovine plasma (Delavaud et al. 2000). In brief, recombinant ovine leptin was used for preparation of both iodinated tracer (~20,000 cpm/tube) and standards (range 0.006 to 0.031 nmol/tube). The primary antibody (Ab# 7137) was used at a final dilution of 1:30,000. Standards were assayed in quadruplicate and samples in duplicate 200 μ l volumes. Displacement of ¹²⁵I-labelled ovine leptin with 30 to 250 μ l of bovine plasma resulted in curves that were parallel to the ovine leptin standard curve. Assay sensitivity and intra-assay CV were 0.03 nmol/L and 3.1% respectively. Serum concentrations of prolactin was determined by radioimmunoassay procedures previously validated at the university of Missouri (Lutz et al. 1991). Minimum detectable concentrations of the hormones in serum were 1.19 ng/tube. Inter-assay coefficient of variation was 17.2% and Intra-assay coefficient of variation was 9.2%.

Statistical Analysis

Data was analyzed using two-way repeated-measures ANOVA procedure and standard least squares model fit (JMP[®], SAS Institute Inc., Cary, NC). Components of the statistical model included breed, time, and treatment by time interactions. When ANOVA revealed a significant difference in least square means, a Tukey-Kramer multiple comparisons test (Steel and Torrie, 1980) was performed at $P \leq 0.05$. Mean differences were determined using Fisher's least significant difference. This was

accomplished using standard errors from the proc mixed procedure of SAS (SAS Inst. Inc., Cary, NC).

Results

Thermoneutrality

Respiration rate at thermoneutrality was higher ($P < 0.001$) in AG than RO by ~20 BPM (Fig 3.2). There was a breed x day x time of day interaction ($P < 0.001$) at thermoneutrality, with the RO showing no change and the AG slowly adapting or reducing respiration rate over time (60 bpm to 40 bpm).

Angus steers also maintained a higher T_{re} (~0.5°C) than RO at thermoneutrality ($P < 0.0001$; Fig. 3.3). Skin temperature across all skin sites were lower for RO than for AG steers, with the greatest differences being at the extremities (lower tail 26.7°C, RO; 28.1°C, AG; Figs. 3.4-3.8). Even toward the trunk of the body, RO steers demonstrated a lower T_{skin} (shoulder 28.6°C, RO; 29.5°C, AG; $P < 0.05$; Fig. 3.5). Similar results were found for sweat rates with AG being ~10 g/m²h higher than RO were also obtained (Fig. 3.9). All variables were stable with exception of respiration rate, which stabilized within 5 days to result in a steady baseline. All measured avenues of heat loss and T_{re} at thermoneutrality were less for RO than AG prior to heat stress, suggesting alternative means of temperature regulation.

Heat Stress

Both breeds increased respiration rate during the first week of heat stress, with AG steers exhibiting the higher rate (60 bpm, AG; 38 bpm, RO; $P < 0.0001$; Fig 3.10).

Respiration rate was not different from the first to second week of heat stress, but the breed differences remained (61 bpm, AG; 42 bpm, RO; Fig. 3.10).

Both breeds showed a sharp increase in T_{re} during the first 3 days of heat exposure (Fig. 3.11). Rectal temperature was maintained higher for AG even after the adaptation period (38.6 versus 38.3°C; $P < 0.0001$; Fig. 3.11). In addition, T_{re} of AG continued to increase during the second week of heat stress while those for RO remained constant (38.7 versus 38.3°C; $P < 0.01$).

One of the most unexpected results was no breed difference in T_{skin} at any site during heat stress ($P = 0.78$; Figs. 3.12-3.16). Skin temperature increased during heat stress for both breeds ($P < 0.0001$), but RO steers displayed the greatest increase. All skin sites for RO steers increased from below AG levels at thermoneutral to the same level as AG during heat stress (AG = $\sim 7.0^\circ\text{C}$, RO = $\sim 8.0^\circ\text{C}$ from thermoneutral). Skin temperatures rose and fell with air temperature among all skin sites. Circadian rhythms were consistent among all days with the lowest recorded T_{skin} at 0600 and the highest at 1600.

Both breeds initially increased sweat rate (4-fold) during heat stress but with a greater increase in AG (292.6 versus 175.23 g/m²h; $P < 0.0001$; Fig. 3.9). This was followed by reduction after 7 d ($P < 0.0001$; Fig. 3.9), and no return to baseline level. However, AG retained a higher sweat rate even after the adaptation period (200.5 versus 110.3 g/m²h; $P < 0.0001$; Fig. 3.9). Reduction in sweat rate coincided with the increase in T_{re} that was stated above for AG cattle. Romosinuano cattle also maintained a lower sweat rate after adaptation, but unexpectedly T_{re} did not increase.

Sweat rate was higher at the shoulder versus the rump regions during heat stress for both breeds (Fig. 3.9). Sweat rates in the shoulder and rump regions for AG and RO paralleled each other during the first week of heat stress, with AG having the higher rate. During the second week of heat stress, all steers showed adaptation with a reduction in slope of sweat rate versus T_a (Fig. 3.17). Although AG maintained the higher rate, they converged as T_a approached 25°C. Angus also maintained a higher respiration rate over RO during both the first and second weeks of heat stress. Unlike sweat rate, there was little adaptation (Fig. 3.18). Similar to respiration rate and sweat rate, AG maintained a higher T_{re} which did not correlate well with T_a ($P > 0.10$; Fig. 3.18).

All measured parameters were evaluated to determine correlation coefficients and predictors of heat stress between the two breeds. Most variables were highly correlated with T_a . Skin temperatures were highly correlated between themselves and with T_a for both breeds ($r = 0.88$). Respiration rate also showed a good correlation with T_a . However, AG steers had a much higher correlation with T_a than RO steers ($r = 0.70$ versus 0.57). Rectal temperature showed a very poor correlation with T_a . Even with the poor correlation, AG steers still showed a much higher correlation compared to RO steers ($r = 0.32$ versus 0.14). Rimosinuano steers seem to regulate T_{re} nearly independent of T_a .

Sweat rate was compared with T_a and T_{skin} to see which is the best indicator or predictor of sudomotor activity. Air temperature showed the best correlation with both shoulder, however T_{skin} also was highly correlated (Table 3.2). Angus steers showed the greatest correlation between shoulder sweat and T_a ($r = 0.73$ versus 0.64; Fig. 3.19). Shoulder sweat rate versus T_{skin} showed a similar result, with AG having the higher correlation ($r = 0.70$ versus 0.59; Fig. 3.20). Rump sweat rate correlations with T_a and

T_{skin} were much closer than shoulder sweat rate (Table 3.2). Again, AG showed the highest correlation with both variables (T_a $r = 0.71$ versus 0.65 ; T_{skin} $r = 0.70$ versus 0.52 ; Figs. 3.19 & 3.20). Using these correlations, it is clear that AG steers were more affected by an increase in T_a . Using broken line analysis in SAS (Proc nonlinear model), we see similar results. Angus steers had a lower break than RO (give values), suggesting they increase cutaneous evaporation earlier and at a lower T_a and T_{skin} . Shoulder sweat rate showed a T_a break of 24.58°C for AG and 27.16°C for RO. Skin temperature also showed a T_a break that was higher in AG (31.58 versus 33.95°C). Rump sweat rates were much closer together with a break occurring at 24.56°C for both breeds. Rump sweat rate versus T_{skin} was also close giving a break point of 32.86°C in AG and 34.13°C in RO. These break points do illustrate an interesting picture and reinforce the results derived from correlation coefficients, but there was a large variance in these points giving no significant differences between breeds. Even use of break point analysis on individual animals produced a large variance. Therefore, values used in this paper are averages for each breed.

Several blood analyses, including CPK, urea nitrogen, potassium, chloride, glucose, and globulin, showed no breed or thermal effects (Table 3.3). Other blood parameters including albumin, AST, GGT, triglyceride, and prolactin showed no breed differences, but demonstrated heat-induced increases for both breeds ($P < 0.05$; Table 3.3). Breed differences throughout the study were seen for ALT, calcium, cholesterol, creatinine, and leptin concentrations ($P < 0.05$). The most interesting of these responses were those that showed thermal by breed interactions. These variables include creatinine, cholesterol, prolactin, sodium, and total protein ($P < 0.05$; Table 3.3). Angus steers

demonstrated heat stress-induced increases in prolactin, creatinine, and cholesterol ($P < 0.05$), but showed no breed differences at thermoneutrality. Sodium and total protein also showed different responses for AG steers, with increasing concentrations, and RO steers, with decreasing levels with heat stress (Table 3.3).

Discussion

The most commonly used variable to assess heat tolerance is T_{re} . Since T_{re} of different breeds is easily assessable in the literature and is moderately heritable (.33; Turner, 1984), it makes a reliable index. In a study by Hammond et al. (1996), AG heifers were contrasted with Brahman, RO, and Senepol heifers. They found that T_{re} in AG was greater than the three other breeds on the hottest day of summer. Even when T_a was much cooler in the winter, T_{re} of the AG remained greater than in RO or Senepol breeds. Although significant, the magnitude of these differences in winter was only 0.5°C at the most (Hammond et al. 1996). These results are consistent with those found in the present study. Whether under thermoneutral conditions or during heat stress, AG maintained a 0.5°C higher T_{re} . Even with this difference in T_{re} , AG cattle still showed an ability to regulate core body temperature well below 40°C .

Steers in the present study showed a linear increase in T_{skin} with T_a . Romosinuano steers, which maintained a lower T_{skin} than AG steers at thermoneutrality, were not different from the AG during heat stress. This phenomenon has been reported by others for *Bos indicus*-type cattle. Allen (1962) compared Brahman and Jersey cattle T_{skin} and respiration rates at T_a from 24 to 35°C . He reported that *Bos indicus*-type cattle had the lower T_{skin} below T_a 24°C and the higher mean T_{skin} above T_a 35°C . He also found that

Bos indicus-type cattle had a lower respiration rate at all levels of T_{skin} . When T_{skin} is above T_a , heat loss by radiation, conduction, and convection all increase. The rate of cutaneous evaporation from the skin also increases as T_{skin} increases. Therefore, the increase in T_{skin} in the present study is advantageous to both breeds, as long as T_{skin} is below core temperature to maintain the outward flow of heat. The lower T_{skin} of RO at thermoneutrality is also advantageous, as the heat loss is minimized when heat conservation is important to the animals. Another possibility is that the air temperature was a cool temperature for the RO steers. It may be that what is considered thermoneutral for AG steers is below thermoneutral for the RO steers which would cause vasoconstriction. Heat flow at the skin was not measured, but using the thermocirculation index as an indicator of heat flow showed a tendency for lower blood flow to the skin of the RO steers ($P=0.07$). Many *Bos indicus* breeds are known for having a number of anatomical and physiological features that improve heat loss from the skin. These include greater blood flow to the skin facilitating heat transfer to the surface (Finch, 1986), lower resistance to internal heat transfer thus allowing heat to be removed via the skin (Finch, 1985), and shorter hair coats (Finch, 1986). It is reasonable to think that RO steers may make use of these *Bos indicus* attributes.

Respiration rates for AG during the first week at thermoneutrality were elevated above RO level, which is likely due to a change in environment or other stresses. However by the end of the first week, respiration rates were similar to what others have reported at thermoneutrality (Gaughan et al., 1999). The RO steers showed no such reduction, consistent with the breed being known as a docile breed (Chase et al., 1997). They maintained a respiration rate lower than Angus steers and closer to what others have

reported for Brahman steers (Gaughan et al., 1999). Both breeds increased respiration rates during heat stress. Elevated respiratory evaporative heat loss, as evidenced by increased respiratory rate, is one part of many avenues used by cattle to increase heat loss in situations of elevated heat load (Hales and Findlay, 1968; Hales, 1976). It is known that respiration rate or panting in cattle has varies among individuals within a single breed (Bianca, 1963). However, Robertshaw (1985) suggests that respiration rate may still be a more appropriate indicator of heat stress than internal temperature. Respiration rate during heat exposure is known to increase more rapidly than other responses and often occurs at a lower critical T_a than other responses such as rectal temperature or changes in feed intake (Hahn, 1999). McDowell (1972) stated that increased respiration rate is the first outward indication that a cow is responding to increased thermal load. In addition, respiration rate (i.e., respiratory evaporative heat loss) is one of a number of effectors responses, including sweat rate and peripheral vasodilation, which determines the internal body temperature response to heat stress. In theory, it is only when the avenues for heat loss are compromised, or limits of effectiveness are reached, that one would see an increase in internal body temperature. Evidence in the present study suggests that an increase in internal body temperature may occur prior to this point and even after some heat loss avenues are reduced.

In the present study, AG cattle showed a higher respiration rate at thermoneutrality and under heat stress conditions than the RO cattle. This is consistent with the results found in other studies (Spiers et al., 1994; Hammond et al. 1996). It is known that *Bos indicus* breeds, specifically, have a lower respiration rate compared with most *Bos taurus* cattle. In a study conducted by Turner (1980), he attributed the lower

respiration rate in Brahman to differences in certain hematological variables. Brahman cattle have been shown to have a higher PCV and erythrocyte number compared with British *Bos taurus* breeds (Howes, 1963), which suggests a greater oxygen-carrying capacity consistent with lower respiration rate. Since RO cattle appearance and heat tolerance are similar to Brahman cattle, they may also have similar hematological values. This could offer some explanation for the differences in respiration rate between the two breeds in this study at thermoneutral conditions. However, under conditions of heat stress, it would appear that metabolic heat load would account for the respiratory rate differences.

Previous research (Hammond et al. 1996; Spiers et al. 1994) has shown that RO steers have a superior thermoregulatory ability compared to AG cattle. This ability must be the result of either a reduction in heat production, increased capacity for heat loss to the environment, or some combination of both. In the present study, all measured heat loss mechanisms were lower for RO steers, suggesting that a lower heat production is responsible for the lower core temperature. There is ample evidence that basal metabolic rate of heat tolerant *B. indicus* cattle is lower than for *B. taurus* cattle (Hansen 2004). A lower metabolic rate usually results in a reduced growth rate or reduced milk production (Hansen 2004). Results from Chase et al. (1997) have demonstrated that RO steers have a slower growth rate than other *B. taurus* breeds again suggesting reduced metabolic rate is maybe a contributing factor to their thermotolerance.

Only one known study has examined sweating rate of RO cattle (Spiers et al., 1994). Their results found that RO cattle showed the superior ability to sweat compared to AG cattle. Coming into this study, expectations were that the RO cattle would have a

higher sweating rate than the AG cattle. Finch (1985) found similar results reporting that when internal body temperature increases, sweating rates are greater and increase more quickly in tropically-adapted cattle than in temperate zone *Bos taurus* cattle, in which sweating rates tend to reach a plateau after the first increase (Finch, 1985). Results from this project contradict their results. However, there are some major differences between the studies that may explain these results. Spiers et al. (1994) only measured sweating rate twice during their experiment. They also placed the animals in a constant heat stress compared to the cyclic used in this experiment. While not many researchers have looked at sweat rates in heat tolerant *Bos taurus* cattle, research with *Bos indicus* cattle has been conducted since the 1930's. *Bos indicus* cattle have been shown to have lower sweating rates than *Bos taurus* cattle under mild conditions, but higher rates at higher levels of stress under acute conditions. With no night-time cooling in the study conducted by Spiers et al. (1994), its fair to say they may have been under a larger strain. Results from Rhoad (1940) and Allen et al. (1963) confirm this phenomenon.

Yeck and Kibler (1956) found a similar result, reporting that less heat-tolerant breeds drew on evaporative cooling reserves at moderately low T_a and were less able to increase vaporization rates at higher T_a . In a follow up study, Kibler and Yeck (1959) showed that surface vaporization ranking of Shorthorn, Santa Gertrudis, and Brahman breeds at 18.3-26.7°C was reversed at higher temperatures with Brahman having the higher rate. Similar to results between this study and Spiers et al. (1994), not all investigators have found higher heat-induced sweating rates in *Bos indicus* cattle compared to British types (Kibler and Brody 1952; McDowell et al., 1954). Variations in

such factors as heat production, coat cover, and acclimatization complicate comparisons and maybe responsible for these different results.

Differences in sweat rate may also be due to the functionality of sweat glands. There are known differences in sweat gland parameters, as well as morphology (Nay and Hayman, 1956). Yeates et al. (1975) reported that tropically-adapted *Bos indicus* cattle have baggy-shaped sweat glands, whereas *Bos taurus* breeds have tubular sweat glands. Yeates et al. (1975) also reported that smaller baggy-shaped glands are present in Jersey cattle, which are known to be more heat tolerant than other *Bos taurus* breeds. In a study conducted in Brazil, Carvahlo et al. (1995) found that even though imported Simmental cattle had a sweat gland activity that was similar to that of *Bos indicus* cattle, cooling rates were higher in *Bos indicus*. This study also found differences between native and imported Simmental cattle. Native Simmental cattle had smaller sweat gland perimeters (length and width), but the glands present were more active, supporting the statement made by Yeates et al. (1975) that baggy-shaped sweat glands present in certain *Bos indicus* cattle are more active than other types of sweat glands. It may be that AG from Florida posses this active baggy-shaped sweat gland, giving them a greater ability to sweat.

One of the most unexpected results was a reduction in sweating rate after 7 days of cyclic heat stress. As very few studies have looked at sweating rates over long-term heat stress, this decrease has never been reported. Interestingly this reduction in sweat rate coincided with the increase in maximum T_{re} for AG steers, suggesting water or mineral balance may be more important than core body temperature regulation. Finch (1986) reported that a widening of the daily body temperature cycle in cattle arises from

changes in energy and water metabolism. However, while this capacity is an adaptation which promotes survival, there is evidence that cattle which maintain their core body temperature within a very small daily cycle are more productive than those with a wider cycle (Finch, 1986). Since water was available ad libitum, it is unclear why water balance issues would arise. Unexpectedly, RO cattle also maintained showed a reduced sweat rate during the second week of heat stress, but demonstrated no change in T_{re} .

In the present study, T_a showed the greatest correlation with all measured parameters. This study confirms the results seen in Chapter 2 that T_{skin} and respiration rate show good correlations with T_a , while T_{re} , which is the end result of thermoregulatory mechanisms, shows a poor correlation. Comparing shoulder sweat rate versus T_a and T_{skin} showed that T_a had the greater correlation. Skin temperature still showed a good correlation, but still did not appear to be the principle driving stimulus. Relationships to T_a and T_{skin} were the same suggesting that T_{skin} may be the driving stimulus or a good indicator of sweat rate in areas of the cow with low numbers of sweat glands. Driving Stimulus of sudomotor activity was reviewed in Chapter 2. Interestingly, AG steers showed higher correlations coefficients across the board. This again shows that RO steers may have a better ability to regulate their internal body temperature compared to AG steers.

In the present study, blood glucose levels were not different between breeds. Since they were on a maintenance diet this is expected. There was a statistical trend ($P < 0.10$) for it to decrease with heat stress however. There are many reports that blood glucose decreases during heat stress (Koubková et al., 2002; Brody, 1956). Being that both breeds were on maintenance level feed intake, it may be that the feed intake did not

drop as much during heat stress preserving the same level of glucose in the blood. Triglyceride concentrations increased for both breeds with heat stress. Abeni et al. (2007) reported that blood triglyceride level decreases with heat stress. One explanation for the conflicting results may be the difference in the diets. In the present study, steers were fed a maintenance level diet. During heat stress, there was no reduction in feed intake, however metabolism is known to decrease during heat stress (Finch, 1986). Therefore, the increase may be due to the steers becoming more metabolically efficient and ultimately using less triglycerides.

Serum calcium was higher for RO than AG steers throughout. Both groups increased calcium concentration with heat stress. This is an unexpected result since most studies show a reduction in blood calcium with heat stress (Shaffer et al., 1981). The increase in calcium in the present experiment while significant, never reached an abnormal level. Breed differences are also hard to explain as there have been very few studies looking at breed differences in calcium levels among beef cattle. Blood calcium concentration is not always a good indicator of calcium status due to plasma calcium being maintained by homeostatic mechanisms such as reabsorption from bone (NRC, 2000). One explanation may be due to a Vitamin D deficiency which has been shown to increase levels of unabsorbed calcium (Nicolaysen, 1936). Since Vitamin D deficiency can develop from poor dietary intake or limited exposure to sunlight; it could be argued that serum calcium increased due to the lack of sunlight and steers being on a maintenance diet for 4 weeks rather than heat stress. However this is only a speculation.

Very few studies have looked at gamma glutamyl transferase (GGT) in terms of heat stress response. Gamma glutamyl transferase has been used in the overall evaluation

of the health status for specific liver damage (Rico et al., 1977). In the present study, GGT increased during the heat stress for both breeds. Similarly, aspartate aminotransferase (AST) increased with heat stress. Decreases in AST have been reported by Srikandakumar et al. (2003) during heat stress in sheep. Gamma glutamyl transferase and aspartate aminotransferase is not well studied with regards to heat stress, since it is an indicator of health status of the liver. One explanation for these increases may be due to liver biopsys that were taken once a week throughout the project. However, this has not been reported before.

Blood alanine transaminase (ALT) in the present study showed a breed difference with AG steers having the higher concentration. Not much is known about ALT differences between breeds of beef cattle. It is well known that stress, corticoids, and diseases of body tissues and injuries affect ALT activity (Boots et al., 1970). Differences in growth rates are also thought to account for the variations in transaminase activity (Boots et al., 1970). However, this has yet to be proven. This could account for the differences observed in this study.

In the present study, serum creatinine increased with heat stress in AG steers, but showed no change in RO steers. An increase in plasma creatinine during heat stress has been reported in sheep and cattle (Srikandakumar et al., 2003; Koubková et al., 2002). The rate of excretion of creatinine is influenced by the glomerular filtration rate such. Heat stress is known to cause peripheral vasodilation to increase loss of body heat, and reduce the blood flow to the internal organs thus increasing creatinine (Srikandakumar et al., 2003). With a large increase in T_{skin} (ie., blood flow to the skin) with heat stress and no increase in serum creatinine in the RO steers, it would suggest that they have a greater

ability to regulate blood flow to internal organs. They appeared not to be stressed to the same level as the AG steers.

Some measured blood parameters did not change with heat stress and were not different between breeds. These include urea nitrogen, creatinine phosphokinase, magnesium, and chloride. Urea nitrogen can be indicative of dehydration (Schmidt-Nielsen et al., 1952) and protein catabolism (Srikandakumar et al., 2003). Creatinine phosphokinase is indicative of muscle injury or pathological problems (Spears et al., 1986). No change in these parameters gives evidence that there are no pathological problems in muscle or water balance. Both magnesium and chloride are dependant on feed intake and diet. Since both breeds were fed a maintenance diet, the concentrations remained stable throughout the experiment.

Total protein constitutes a portion of the amino acid pool of the body and is believed to be indicative of the nutritional status of the animal. Total protein is made up mostly of albumin and globulin. In the present study, total protein increased with heat stress. This has been shown by others (Shaffer et al., 1978). However, globulin did not change with heat stress, showing that albumin is the factor changing total protein concentration. Like many blood parameters, albumin is not well studied with regard to heat stress, but is believed to be involved with water balance (Parker et al., 2003).

Cholesterol was similar between the two breeds at thermoneutrality. However, AG serum cholesterol showed a significant increase during heat stress, while RO cattle remained unchanged. Though not extensively studied in cattle, it has been reported that cholesterol increases during heat stress (Brody, 1956). Shaffer et al. (1981) reported that circulating cholesterol is influenced by the degree of stress which is consistent with the

hypothesis that the RO steers were not heat stressed to the same level as AG. This is interesting because it has been reported that other heat tolerant breeds have higher cholesterol levels than *Bos taurus* breeds (Olbrich et al., 1971; O'Kelly, 1968). Olbrich et al. (1971) found that the mean serum cholesterol concentration were significantly higher for Zebu than Scotch Highland heifers. O'Kelly (1968) also found that cholesterol, phospholipid, and total lipid levels were all significantly higher in Zebu than British breeds.

In the present study, there were no breed or time differences in serum sodium concentrations. However, there was a time by breed interaction with RO steers having a reduction in sodium concentration, while AG steers showed an increase. A reduction in serum sodium concentration during heat stress is expected and has been described by El-Nouty et al. (1980). This reduction is caused by an increase in urinary sodium excretion due to increased total urinary output. An expanded blood volume due to an increase in water intake could also result in a reduced plasma sodium concentration. We have no explanation for the increase in serum sodium in the present study. Normally, an increase in serum sodium is the result of an animal becoming dehydrated. However in the present study, all steers were given *ad libitum* access to water. We can further rule out dehydration by looking at serum urea nitrogen concentration. An elevated plasma urea nitrogen concentration is observed when the water intake is restricted in camels, (Schmidt-Nielsen *et al.*, 1952) sheep, and cattle (Goodall and Kay, 1968). In humans, a ratio of blood urea nitrogen to serum creatinine is also used for clinical diagnosis of dehydration (Thomas et al., 2003). In the present study, there was no change in urea

nitrogen at thermoneutrality or under heat stress conditions showing no signs of dehydration.

Unlike serum sodium, serum potassium showed no changes. This is expected because potassium is well maintained throughout the body. Some studies, including El-Nouty et al. (1980), found that both sodium and potassium serum concentrations were reduced in cows during prolonged heat stress. Because the majority of potassium is maintained in the intracellular compartment, it is possible that the plasma potassium did not reflect total body potassium stores. This could explain the differences between the results from our study. El-Nouty et al. (1980) suggested that reductions in serum potassium were due to loss of potassium in sweat. Johnson (1970) reported that potassium and sodium in secretions were significantly greater in cattle at T_a exceeding 35°C. Below this T_a , skin secretions contained little electrolyte amounts. Since cattle possess apocrine glands, secretions from the skin of cattle can contain 4 to 5 times the level of potassium compared to sodium. Since the heat stress blood sample was taken during the second week of heat stress; sweat rate had already adapted to a lower level. Therefore, it may be that the dietary potassium in this experiment was enough to offset the losses from the skin.

Changes in serum prolactin concentrations in response to increases in T_a have been extensively studied, and are known to be positively correlated (Schams, 1972; Head et al., 1976; Johnson, 1985; Wetteman and Tucker, 1974). Even seasonal changes in serum prolactin of cattle are known, with greater concentrations during warmer months of the year than during colder months (Schams, 1972; Heads et al., 1976). Though plasma prolactin is known to increase during thermal stress, the mechanism is not well

understood (Johnson, 1985). However, Beede et al. (1982) and Collier et al. (1982) indicated that increasing dietary potassium from 0.64 or 1.08 to 1.64% markedly reduced plasma prolactin in heat-stressed cattle, suggesting that prolactin may be involved in increased potassium and sodium turnover during thermal stress. In the present study, there were no differences in serum prolactin concentration at thermoneutrality which is consistent with other reports (Wettemann et al., 1982; Ohlson et al., 1981). However unlike Weetemann et al. (1982), steers in the current study responded differently to heat stress. Serum prolactin concentrations increased with heat stress for the AG steers. However, no increase was seen for RO steers. Weetemann et al. (1982) reported that concentrations of serum prolactin in both *Bos indicus* and *Bos taurus* heifers that were acutely and chronically exposed to various T_a responded similarly, suggesting that the mechanisms responsible for the control of prolactin in serum are not different. If this assumption is correct, then it would suggest that the RO steers were not heat stressed in the current study. While it is not known why prolactin increases with T_a , it shows the potential for being an indicator of heat tolerance.

Very little is known about breed differences in serum leptin concentrations. In the present study, AG steers showed a higher serum leptin concentration compared to RO steers. It has been shown that plasma leptin is strongly related to adipose cell size and number in cattle (Delavaud et al., 2002). It is also known that treatment of animals with leptin causes a dose-dependent decrease in food intake, loss of body weight, loss of fat depots, and an increase in energy metabolism (Houseknecht et al., 1998). Since RO steers in this study were lighter and leaner than AG steers, it may be that adipose cells played a role in the leptin concentration differences. To our knowledge no one has looked at leptin

in regard to heat stress. In the present study, leptin increased with heat stress. It may be that the increase in leptin helps drive down feed intake during the heat.

By extending the length of heat stress to 14 days and cycling T_a , we hoped to get a better understanding of the RO's heat loss mechanisms. To our surprise, the RO steers appeared not to be heat stressed, only showing a moderate rise in T_{re} . Angus steers however, had a higher respiration rate, sweat rate and similar T_{skin} , but still had the greater T_{re} . This would suggest that AG steers have the greater ability to dissipate heat compared to RO steers. Since not all heat loss mechanisms were measured in the present experiment, it is impossible to definitively state the reason for the RO's lower rectal temperature. From these results, lower heat production and/or a greater ability to vasodilate are the most likely candidates for the superior heat tolerance in RO steers.

Rectal temperature is still a good indicator of heat tolerance. In a study by Mackinnon et al. (1991), they reported that the heritability of a single measurement of T_{re} during the summer is $h^2=0.19$ which indicates that heat tolerance can be improved by selection. However, selection based on a mean of four rectal temperatures ($h^2=0.44$) would give more than twice the rate of response based on a single measurement (Mackinnon et al., 1991). Selection for growth is somewhat in opposition to selection of heat tolerance (Mackinnon et al., 1991), therefore solely selecting for tolerance alone will lead to poorly growing animals. However, adding mature weight with rectal temperature increased the correlation for heat tolerance. One of the objectives of this study was to identify additional markers of heat tolerance. This study has identified prolactin, cholesterol, and creatinine as additional markers that require further research. Leptin also shows the need for further research in regard to heat stress. Using these other variables, in

addition to T_{re} , could allow for improved identification of heat tolerant animals. This will also give a better heritability estimate of heat tolerance than T_{re} alone. Once animals are identified, selection pressure on heat tolerance and growth rate can be applied to increase animal productivity.

Figures and Legends

Ingredients	Diet percentage
Corn	39%
Soybean Hulls	39%
Dried Corn Distillers Grain	20%
Mineral Supplement	2%
Mineral Supplement ingredients	
Lasalocid	1600 g/ton
Calcium	Min 16.60% Max 22.30%
Phosphorous	Min 3%
NaCl	Min 3% Max 18.20%
Potassium	Min 0.10%
Magnesium	Min 1.00%
Copper	1,000 ppm
Selenium	26.40 ppm
Zinc	3,750 ppm
Vitamin A	300,000 IU per lb
Vitamin D3	20,000 IU per lb
Vitamin E	100 IU per lb

Table 3.1. Ingredient list of diet. Fed at 1.6% of BW as-fed.

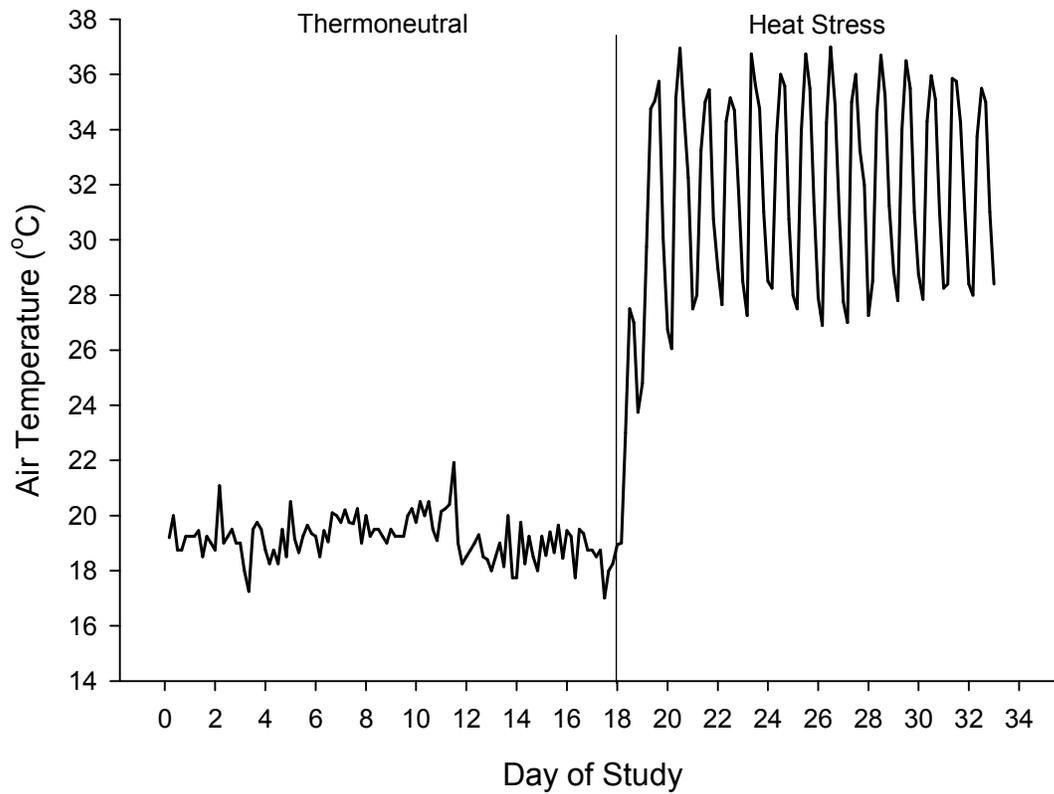


Figure 3.1. Air temperature as a function of time

Thermoneutral Period

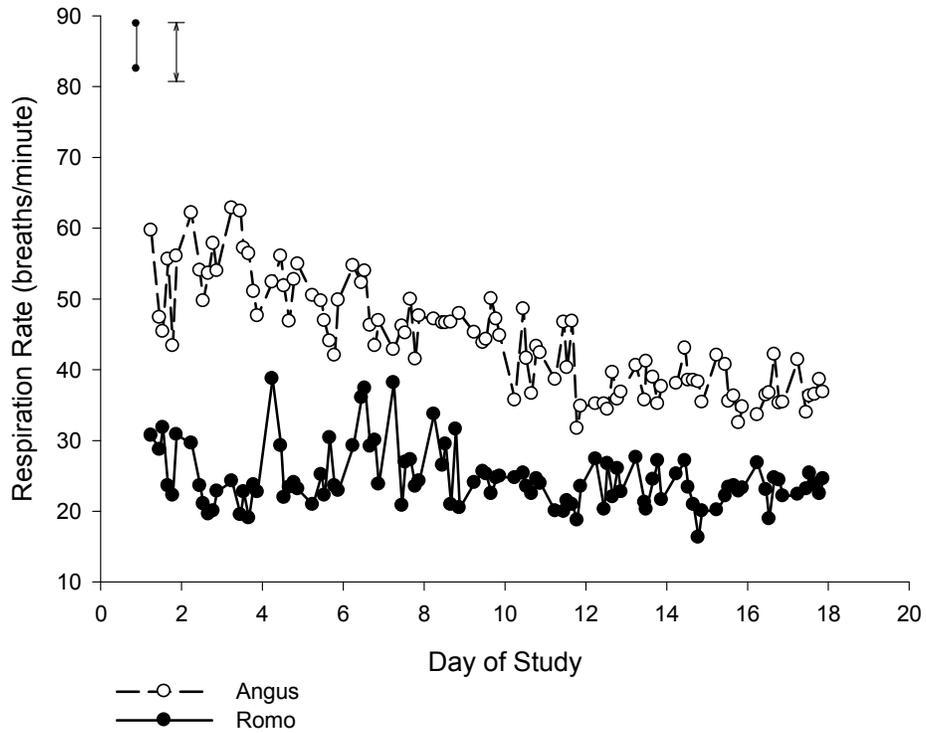


Figure 3.2. Mean thermoneutral respiration rate of Angus and Romosinuano steers as a function of time. \downarrow = LSD within treatment groups \downarrow = LSD between treatment groups

Thermoneutral Period

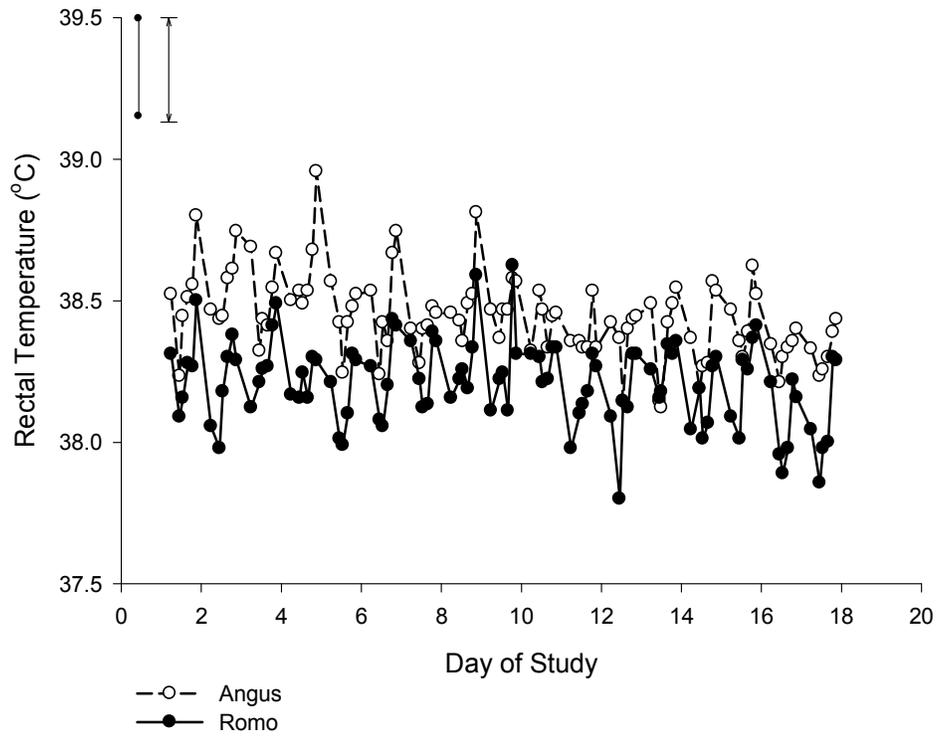


Figure 3.3. Thermoneutral rectal temperature as a function of time. \downarrow = LSD within treatment groups \updownarrow = LSD between treatment groups

Thermoneutral Period

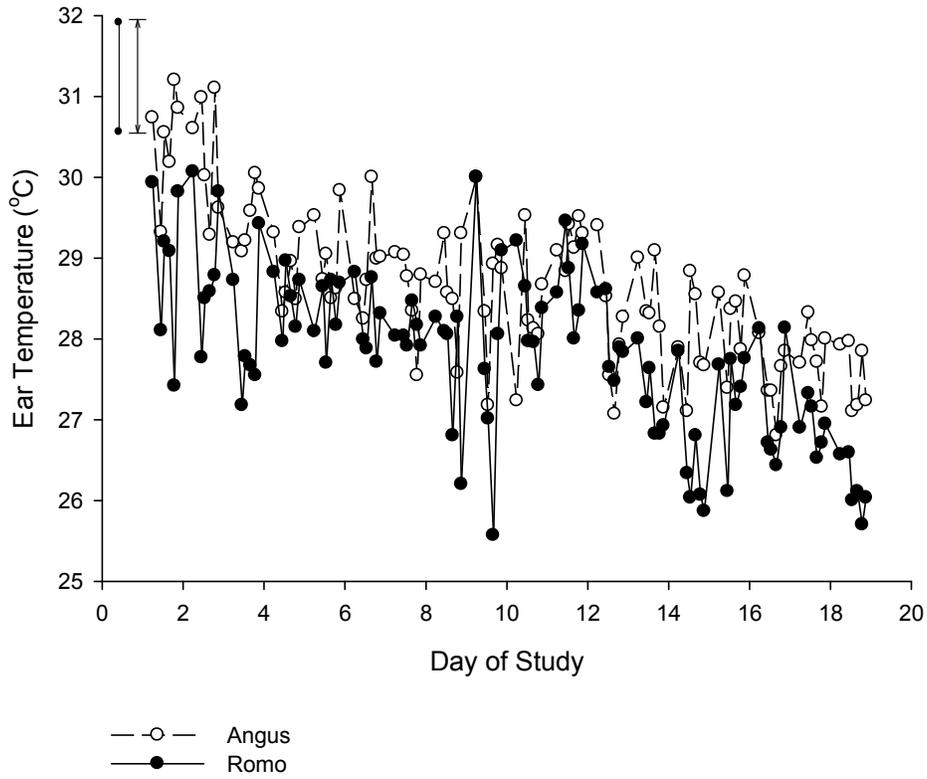


Figure 3.4. Thermoneutral ear temperature as a function of time. \downarrow = LSD within treatment groups \updownarrow = LSD between treatment groups

Thermoneutral Period

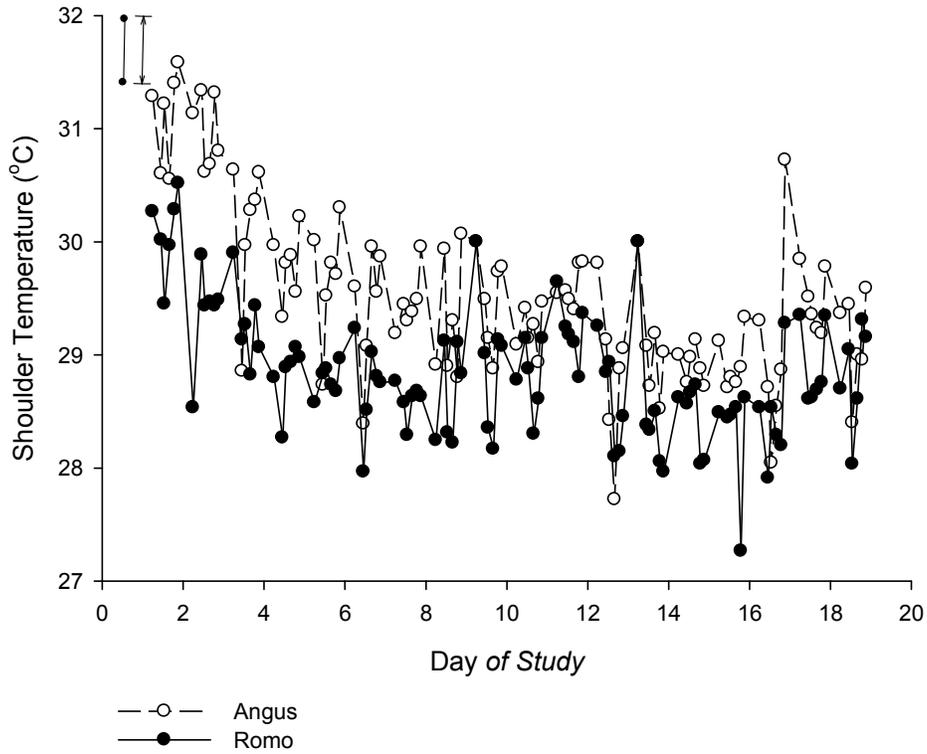


Figure 3.5. Thermoneutral Shoulder temperature as a function of time. \downarrow = LSD within treatment groups \updownarrow = LSD between treatment groups

Thermoneutral Period

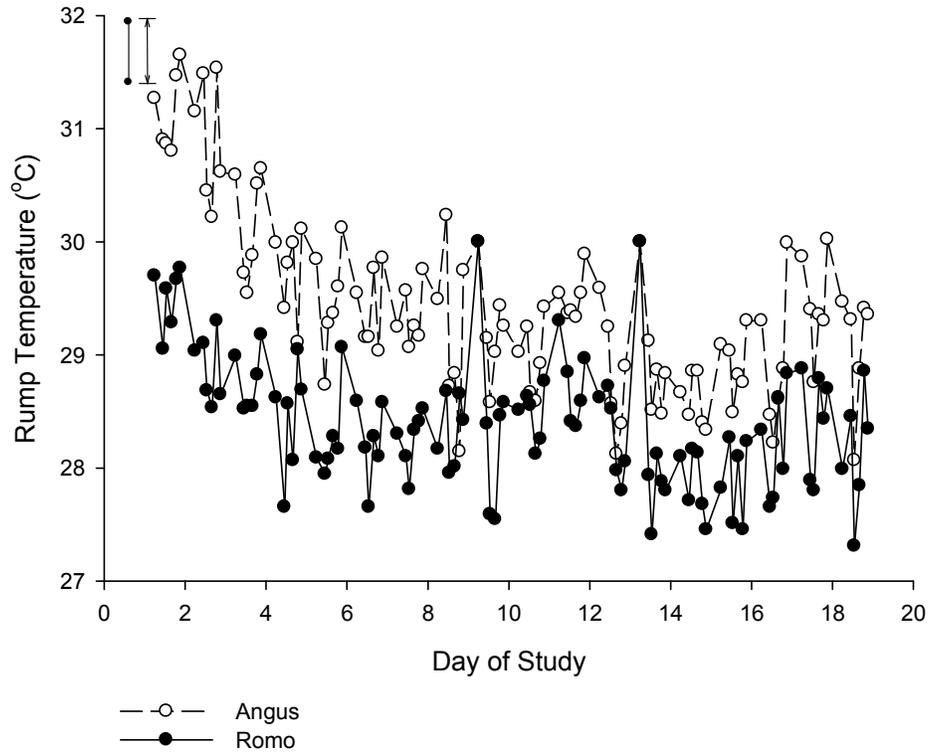


Figure 3.6. Thermoneutral rump temperature as a function of time. \downarrow = LSD within treatment groups \updownarrow = LSD between treatment groups

Thermoneutral Period

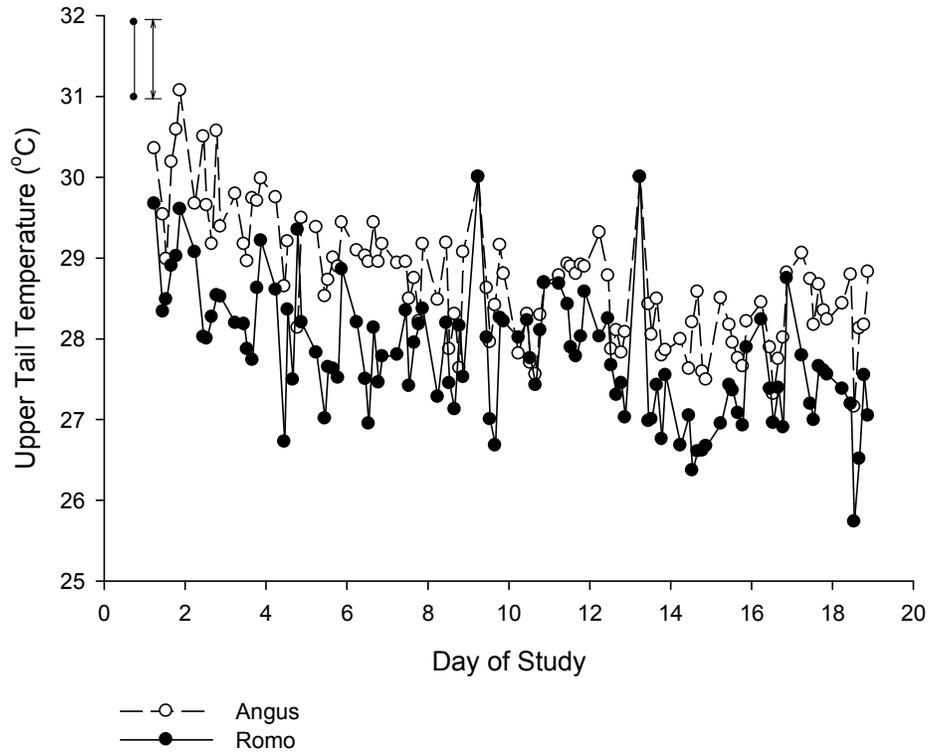


Figure 3.7. Thermoneutral upper tail temperature as a function of time. \downarrow = LSD within treatment groups \updownarrow = LSD between treatment groups

Thermoneutral Period

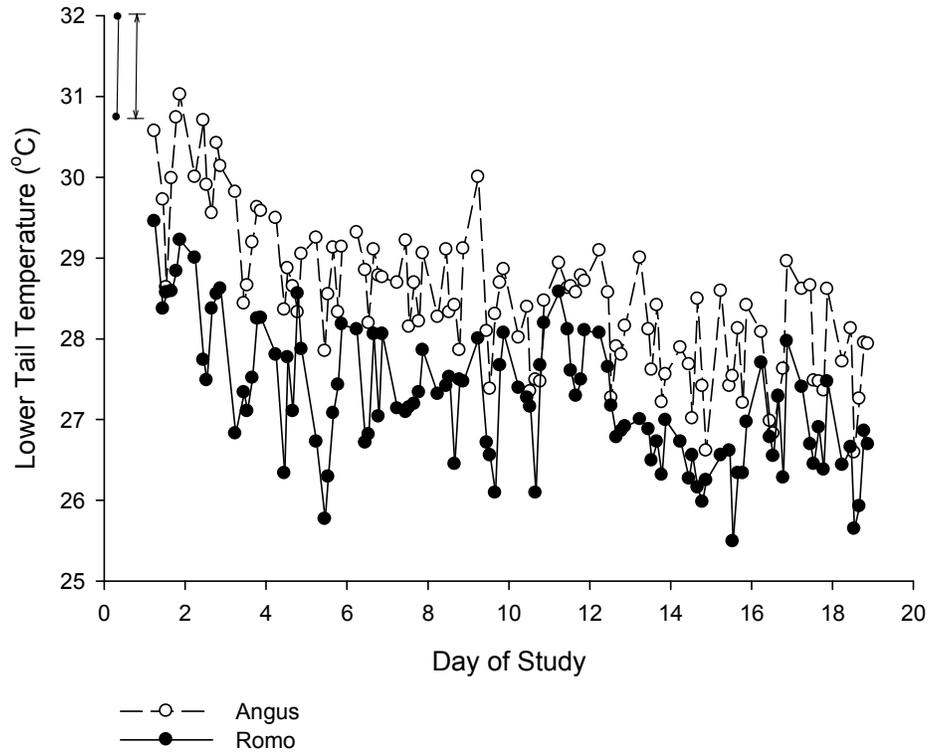


Figure 3.8. Thermoneutral lower tail temperature as a function of time. \updownarrow = LSD within treatment groups \updownarrow = LSD between treatment groups

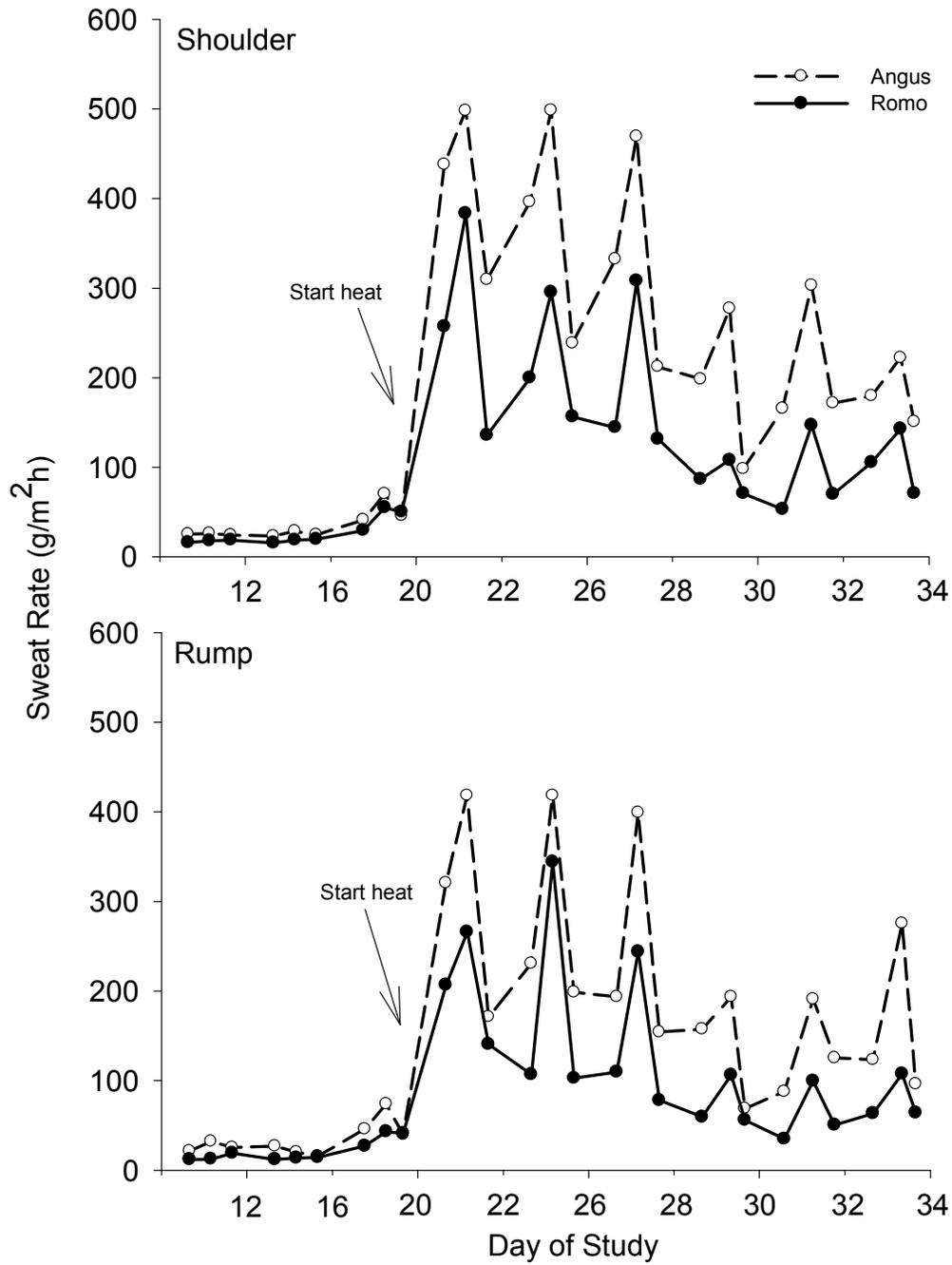


Figure 3.9. a.) Shoulder sweat rate as a function of time b.) Rump sweat rate as a function of time

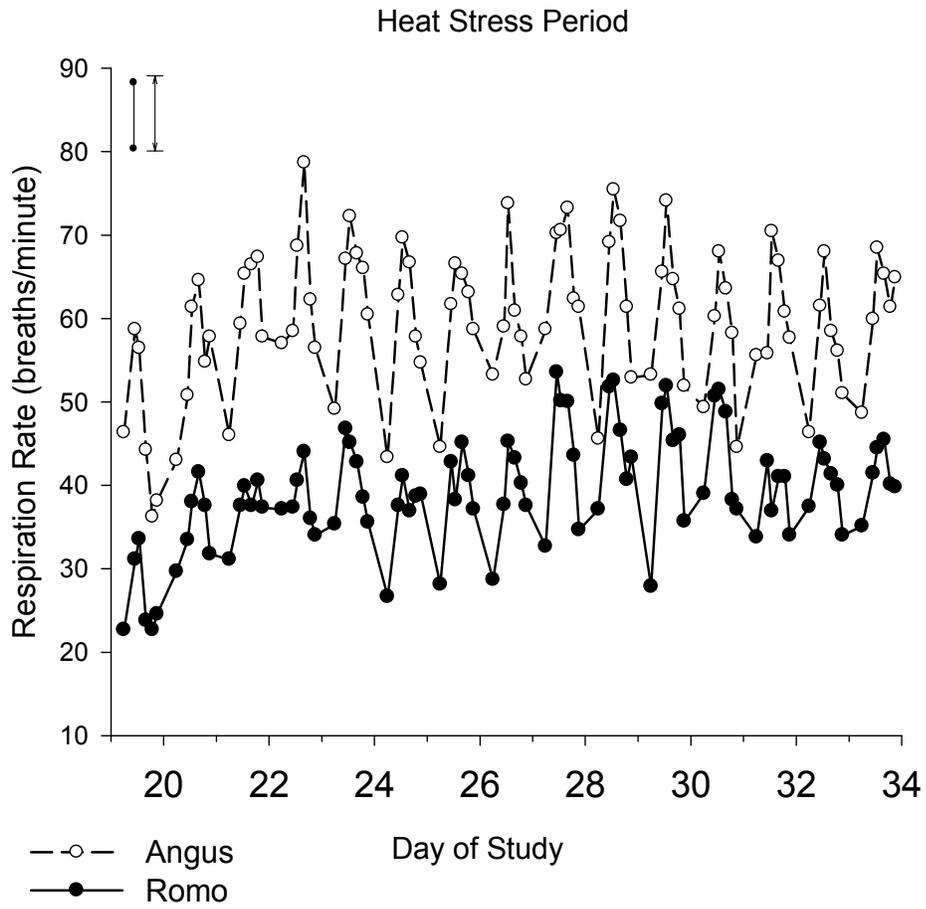


Figure 3.10. Heat stress period respiration rate as a function of time. \downarrow = LSD within treatment groups \updownarrow = LSD between treatment groups

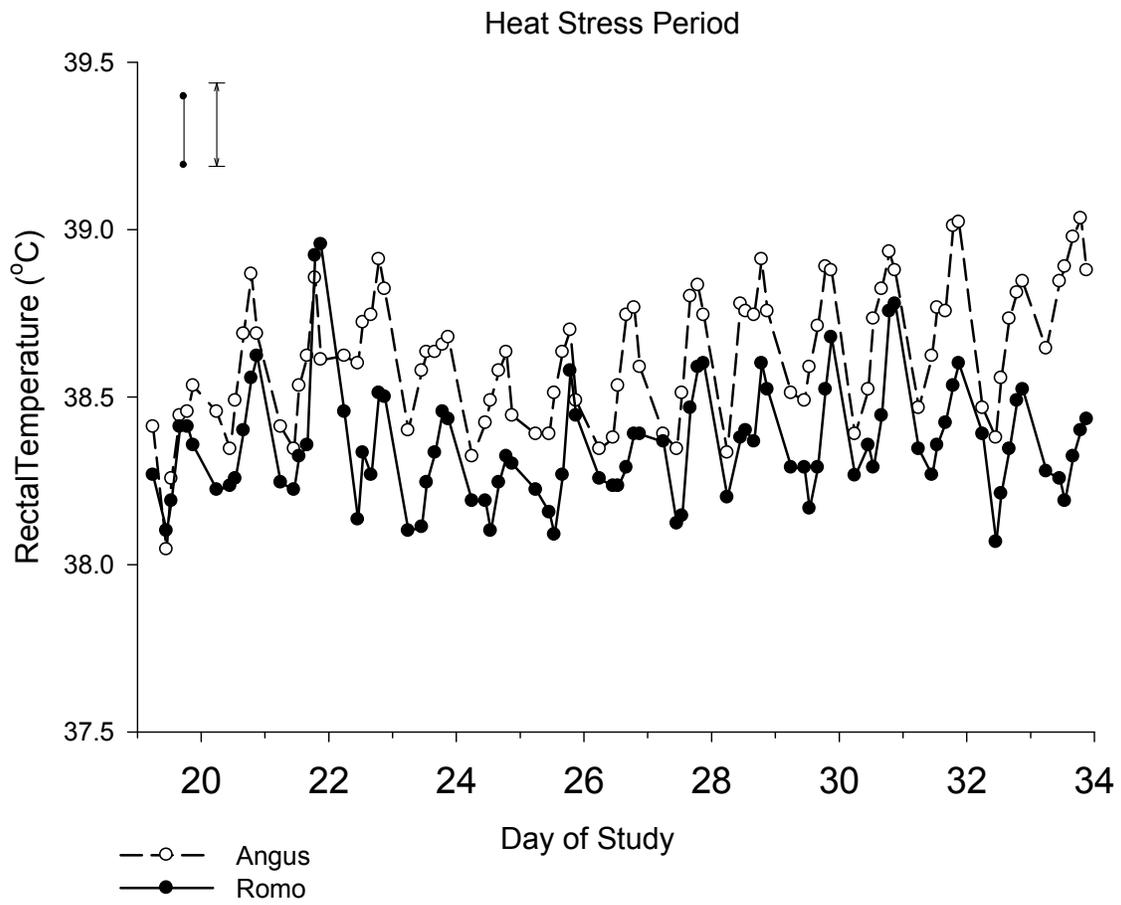


Figure 3.11. Heat stress period rectal temperature as a function of time. \downarrow = LSD within treatment groups \updownarrow = LSD between treatment groups

Heat Stress Period

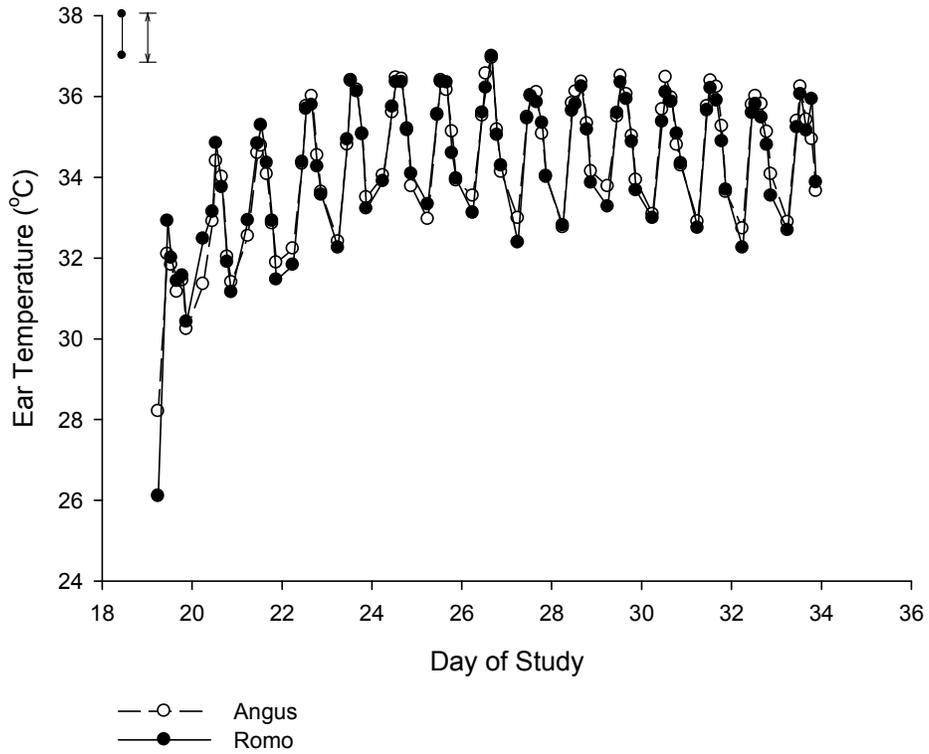


Figure 3.12. Heat stress period ear temperature as a function of time. \downarrow = LSD within treatment groups \updownarrow = LSD between treatment groups

Heat Stress

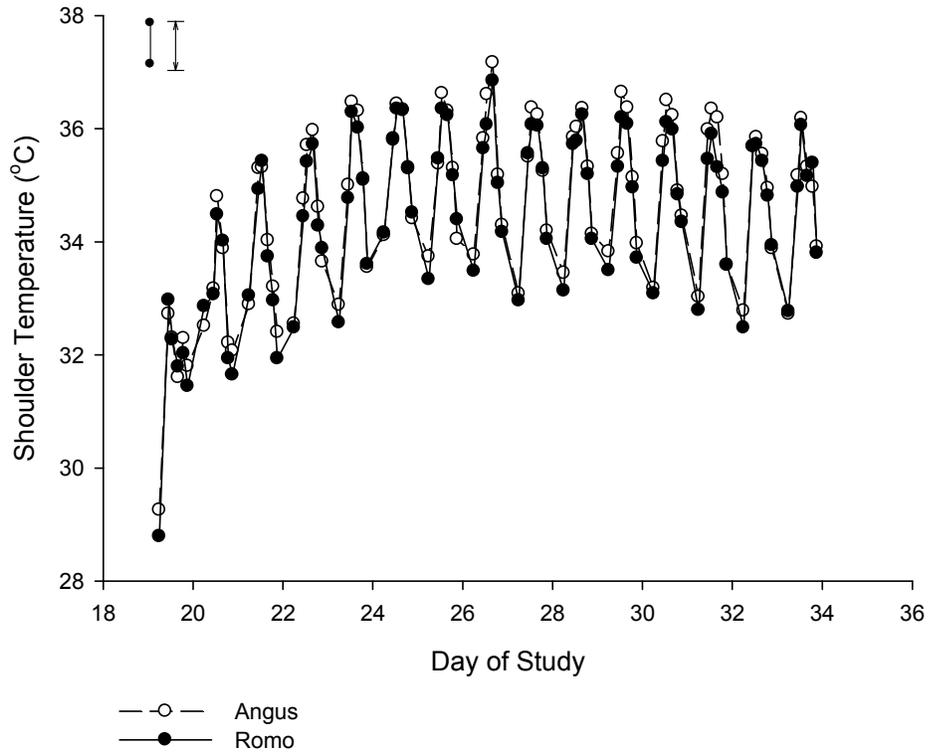


Figure 3.13. Heat stress period shoulder temperature as a function of time. \downarrow = LSD within treatment groups \downarrow = LSD between treatment groups

Heat Stress

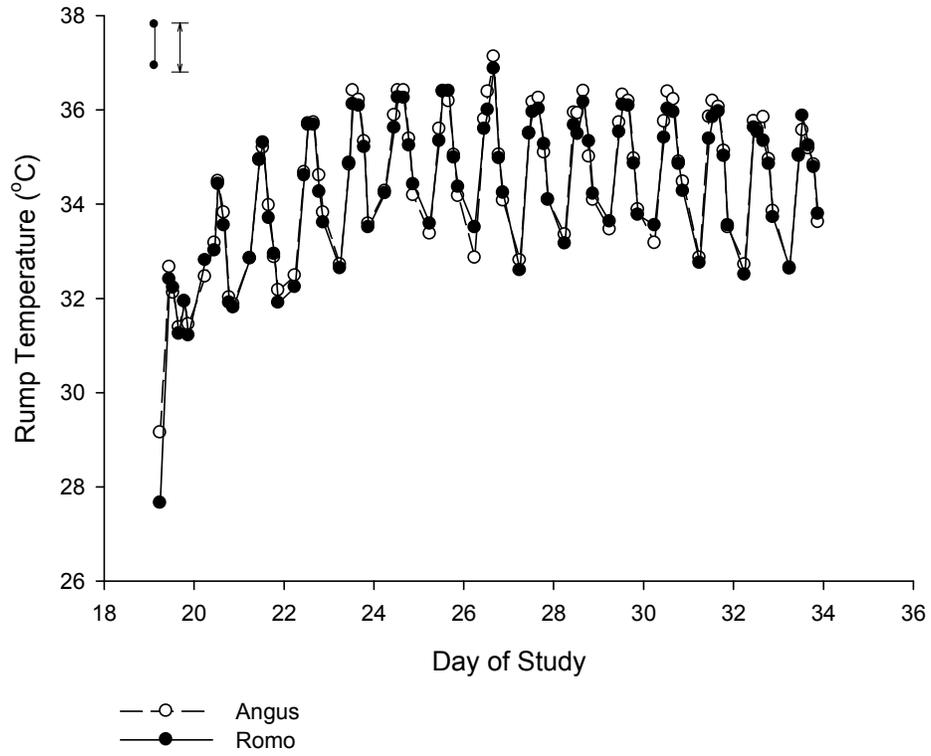


Figure 3.14. Heat stress period rump temperature as a function of time. \downarrow = LSD within treatment groups \updownarrow = LSD between treatment groups

Heat Stress Period

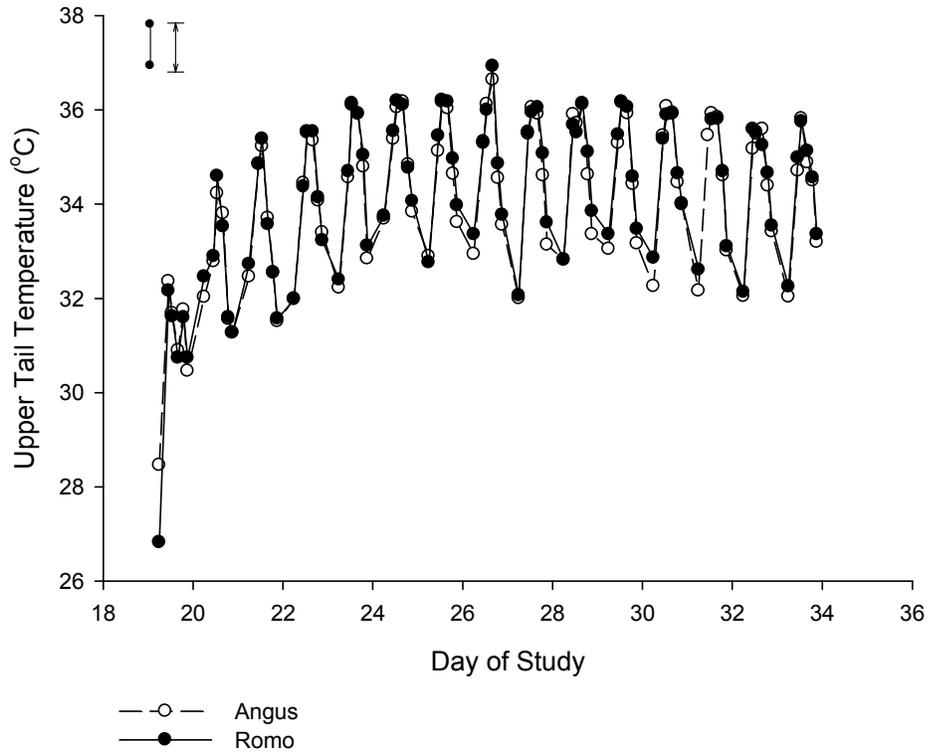


Figure 3.15. Heat stress period upper tail temperature as a function of time. \downarrow = LSD within treatment groups \downarrow = LSD between treatment groups

Heat Stress Period

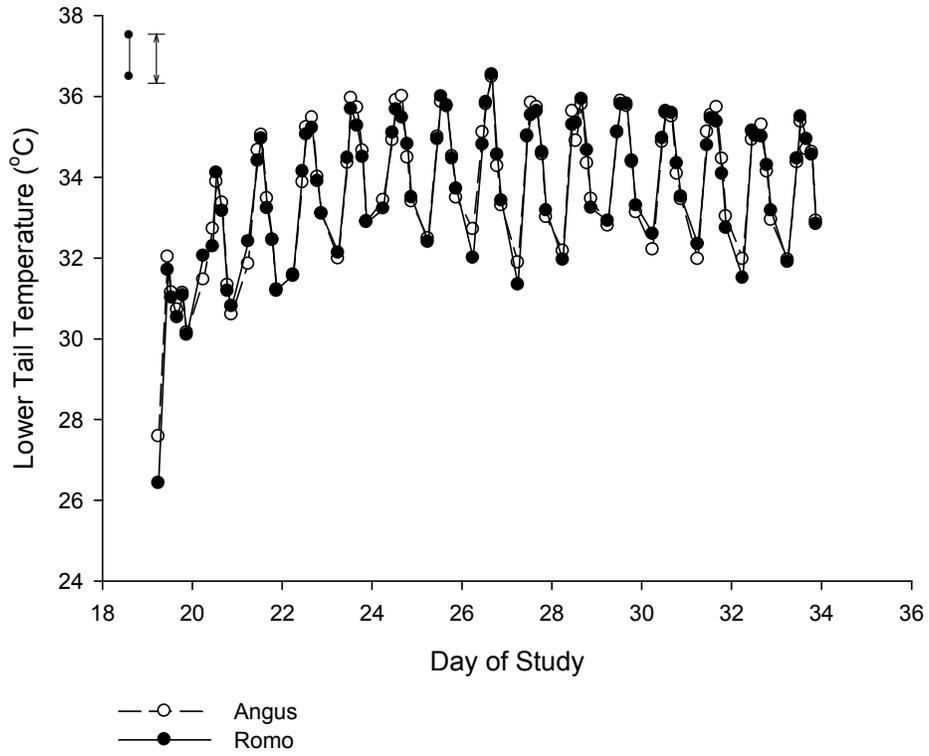


Figure 3.16 Heat stress period lower tail temperature as a function of time. \downarrow = LSD within treatment groups \updownarrow = LSD between treatment groups

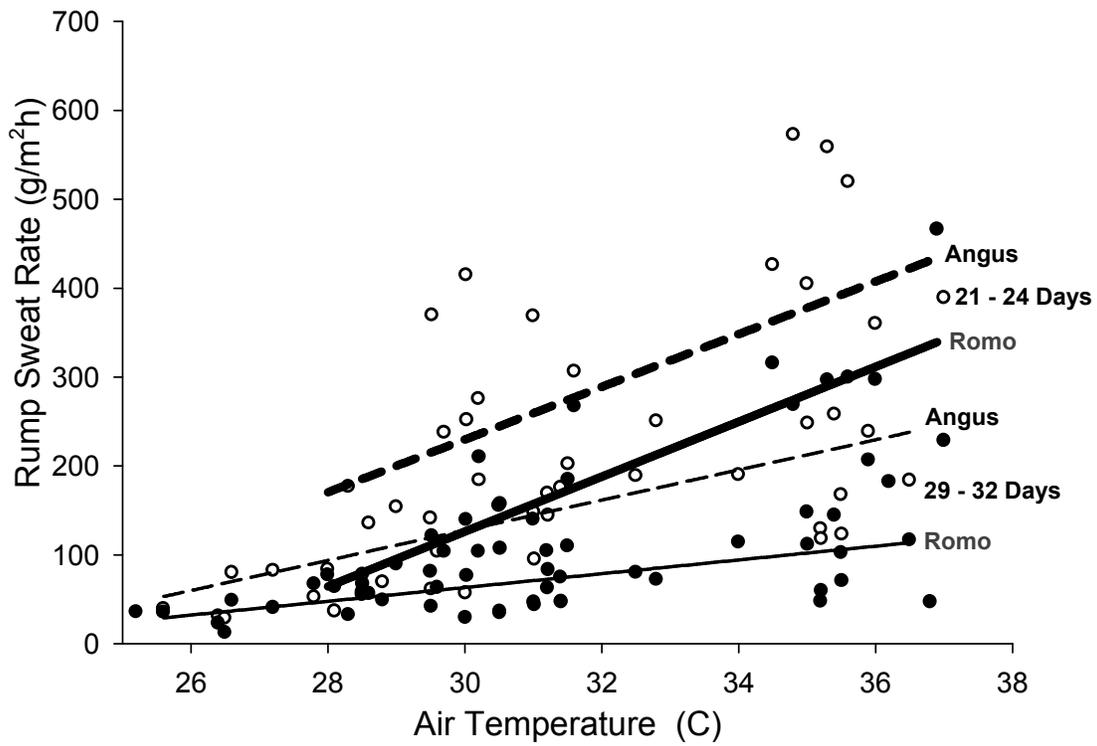
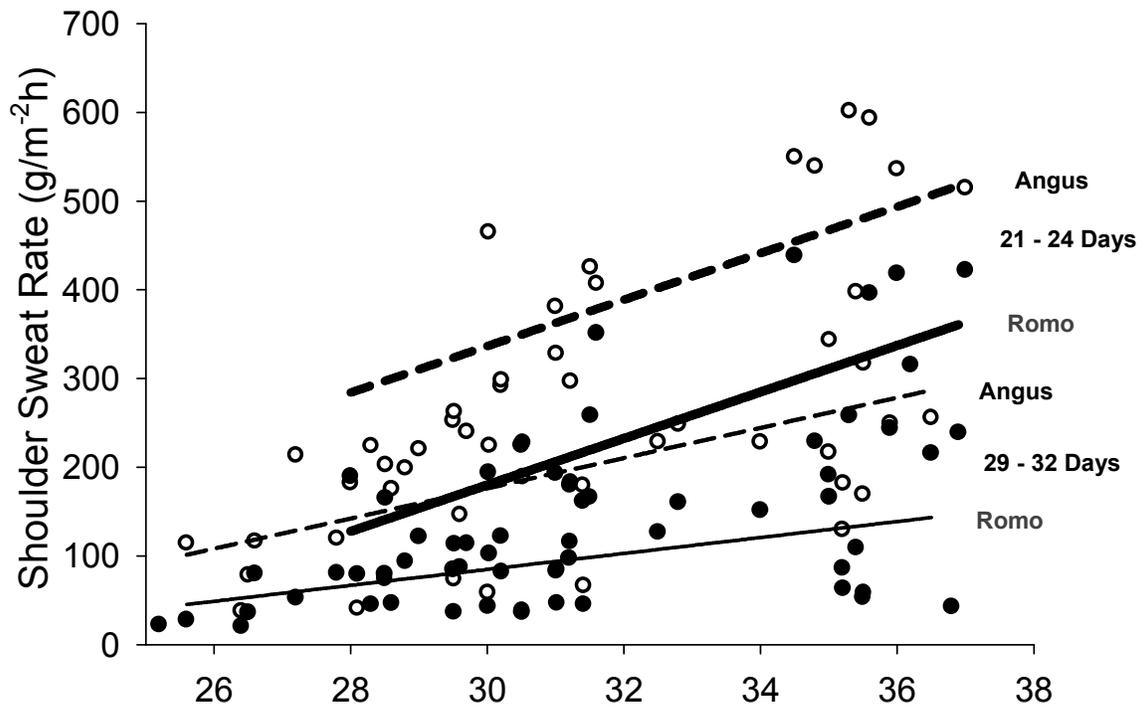


Figure 3.17. Sweat rate vs. air temp. – Early Heat versus Late Heat

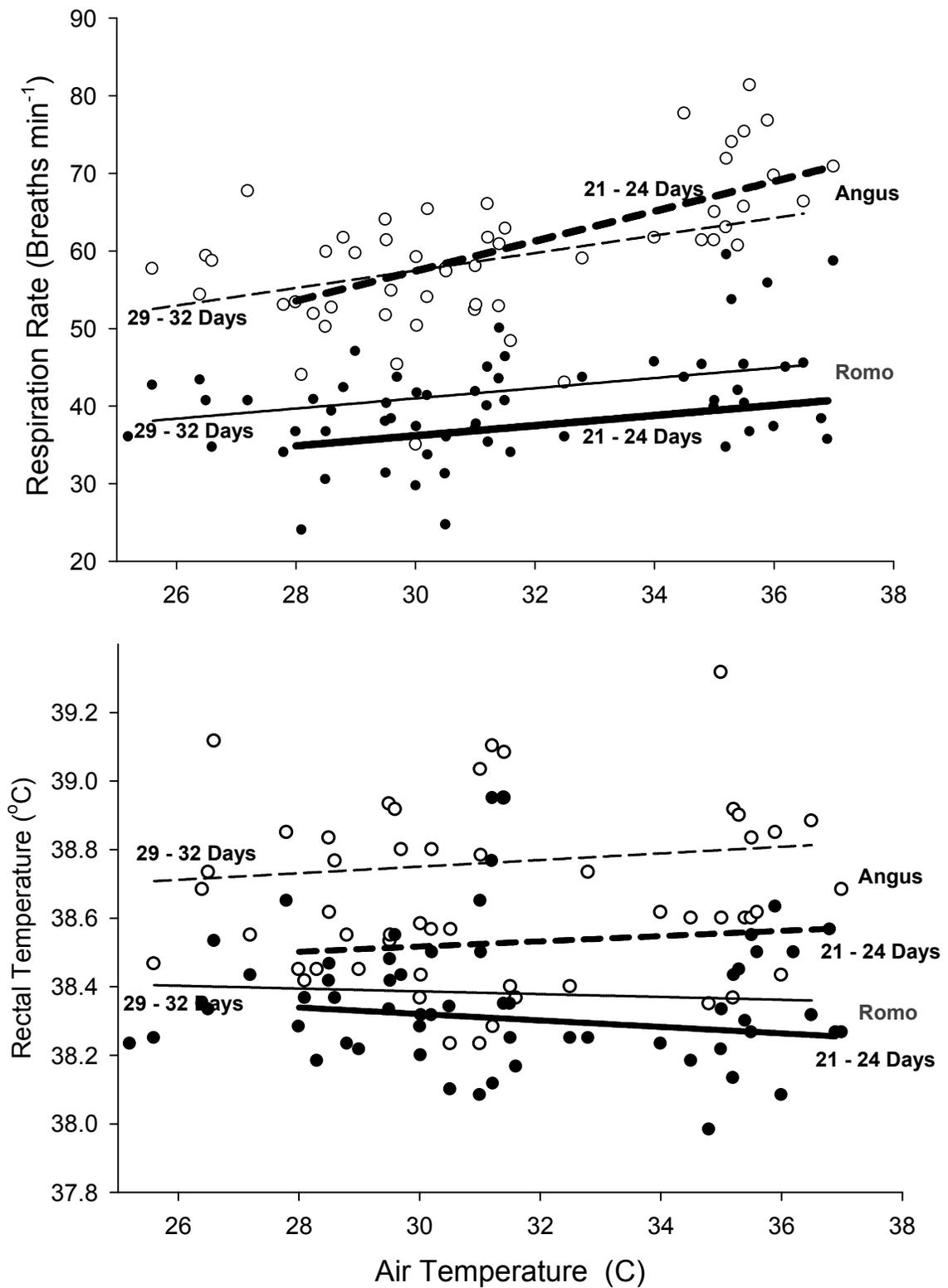


Figure 3.18. Respiration rate and rectal temp. vs. air temp. – Early Heat versus Late Heat

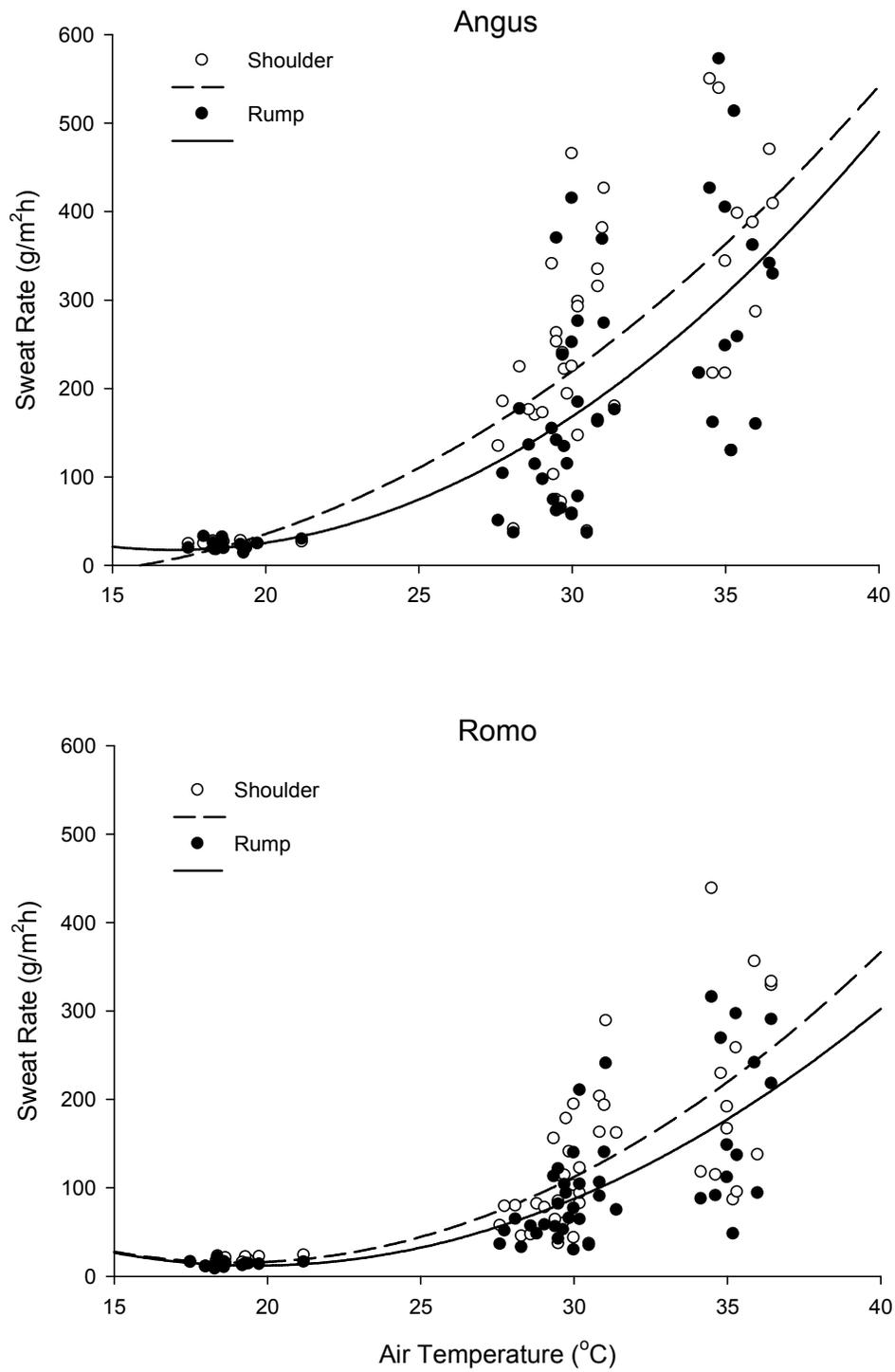


Figure 3.19. Shoulder and rump sweat rate as a function of T_a .

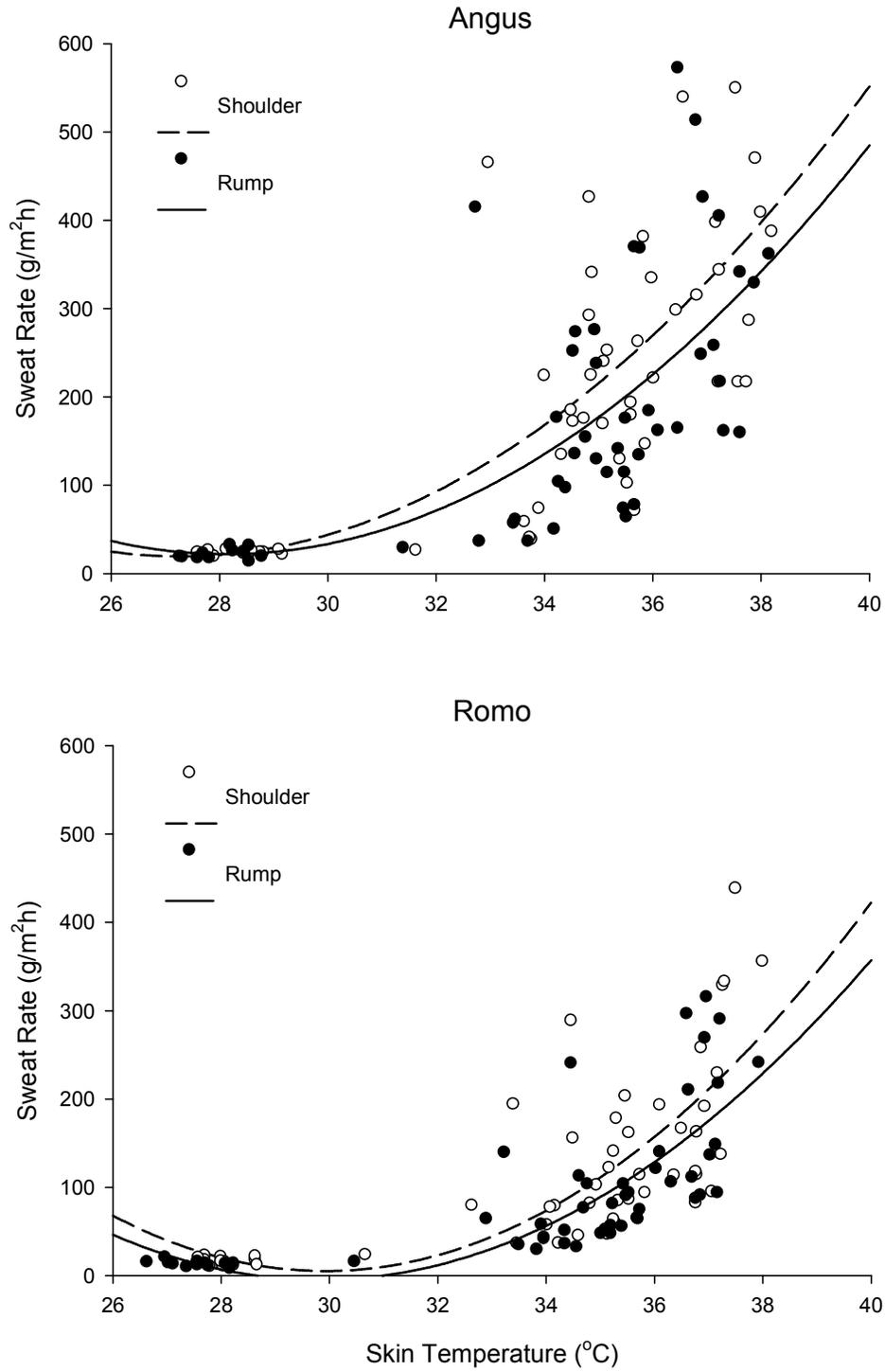


Figure 3.20. Shoulder and rump sweat rate as a function of skin temperature

Variables	Breed	Correlation Coefficient (r)
Respiration vs Air	Angus	.70
	Romo	.57
Shoulder Sweat vs Air	Angus	.73
	Romo	.64
Rump Sweat vs Air	Angus	.71
	Romo	.65
T _{skin} vs Air	Angus	.88
	Romo	.88
Rectal vs Air	Angus	.32
	Romo	.14
Respiration vs T _{skin}	Angus	.71
	Romo	.62
Shoulder Sweat vs T _{skin}	Angus	.70
	Romo	.59
Rump Sweat vs T _{skin}	Angus	.70
	Romo	.52
Rectal vs T _{skin}	Angus	.40
	Romo	.26
Respiration vs Rectal	Angus	.32
	Romo	.20

Table 3.2. Best fit relationship of sweating rates (SR) to air (T_a), skin (T_{skin}), and rectal temperature between breeds

<i>Blood Parameters</i>							
					<i>P Values</i>		
	<i>Breed</i>	<i>TN</i>	<i>HS</i>	\pm <i>SE</i>	<i>Breed</i>	<i>Time</i>	<i>Interaction</i>
Albumin g/dL	AG	3.15	3.45	0.04	0.47	0.001	0.12
	RO	3.28	3.44				
ALT U/L	AG	12.11	13.44	0.81	0.05	0.37	0.47
	RO	10.86	11.00				
AST U/L	AG	54.88	85.66	9.88	0.58	0.01	0.55
	RO	66.73	86.11				
Calcium mg/dL	AG	8.90	9.27	0.10	0.001	0.01	0.51
	RO	9.42	9.66				
Chloride mEq/L	AG	101.78	101.56	1.57	0.13	0.22	0.28
	RO	101.28	97.78				
Cholesterol mg/dL	AG	64.11	91.55	6.17	0.01	0.001	0.001
	RO	58.01	64.88				
CPK U/L	AG	126.44	114.44	20.90	0.80	0.53	0.98
	RO	131.00	118.00				
Creatinine mg/dL	AG	1.16	1.51	0.07	0.01	0.01	0.05
	RO	1.07	1.11				
GGT U/L	AG	12.33	17.55	1.35	0.52	0.01	0.20
	RO	14.85	17.11				
Globulin g/dL	AG	3.08	3.21	0.14	0.90	0.75	0.12
	RO	3.26	3.06				
Glucose mg/dL	AG	77.67	71.78	4.56	0.89	0.06	0.74
	RO	77.63	73.44				
Leptin ng/ml	AG	4.45	5.47	0.38	0.01	0.05	0.56
	RO	3.63	4.22				
Magnesium mg/dL	AG	2.24	2.41	0.06	0.84	0.06	0.32
	RO	2.31	2.36				
Potassium mEq/L	AG	4.31	4.50	0.12	0.28	0.48	0.20
	RO	4.27	4.22				
Prolactin ng/ml	AG	34.11	42.39	1.59	0.1	0.01	0.05
	RO	34.47	36.46				
Sodium mg/dL	AG	141.11	144.44	1.31	0.55	0.95	0.05
	RO	143.63	140.44				
Total Protein g/dL	AG	6.23	6.67	0.16	0.66	0.08	0.05
	RO	6.55	6.51				
Triglyceride mg/dL	AG	15.22	19.22	1.88	0.80	0.05	0.94
	RO	15.64	19.88				
Urea N mg/dL	AG	7.00	6.89	0.67	0.08	0.25	0.32
	RO	6.38	4.89				

Table 3.3. Blood parameters

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