Regional differences in sweat rate response of steers to short-term heat stress

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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 a 24-h time period. Measurements included respiration rate, and air and body (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 chambers. However, respiration rate nearly doubled in the heat ($P<0.05$), increasing when $T_a$ was 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 four-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.

Keywords 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, until the late 1950s it was believed that bovine sweat glands were poorly functional. Worstell and Brody (1953) concluded that cattle, unlike humans, 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 are controversial. Several experiments suggest that skin temperature 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). The experiment presented here addressed three questions: (1) Are there regional differences in sweat rate? (2) How does the thermal environment affect sweat rate? (3) 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 body weight (BW), 8 months old, body condition score (BCS) 4–5] were obtained from the University of Missouri and housed in the Brody Environmental Center (Animal Science Research Center, University of Missouri–Columbia). Animals were maintained at the University of Missouri Beef Farm during winter until December, when they were moved to the environmental 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 × 3.1 m), with water and feed available ad libitum (MFA Cattle Charge, Columbia, MO), for the duration of the study (4 days). Light cycle throughout the study was a 12-h light:dark schedule. The Brody Environmental Center consists of four 6.1 × 9.1 m chambers, two of which were used in the present study. The chambers were divided into three stanchions with each animal loosely restrained to the stanchion by a chain. Air movement in the chamber was held at 15 room changes per hour (4,462 cubic feet of volume).

Procedure

Air temperature (T\textsubscript{a}) was measured by reading a calibrated alcohol thermometer (Fisher S41574R) that was placed in the chamber approximately 0.3 m above the animals in each chamber. Calibration was performed using a traceable digital thermometer (Fisher Scientific-Traceable thermometer 010607). Chamber environmental conditions were controlled using a Fisher-Porter Controller (698B179U01) and a Sensycon I/P Converter (Controller Type 27/06–65). Relative humidity was maintained under 50% during the entire study. Setting relative humidity below 50% reduced the effects of water vapor pressure on thermoregulation and allowed the study to focus on changes in T\textsubscript{a}. The temperature-humidity index (THI) was calculated according to Thom (1959).

Steers were placed in two chambers (three per chamber) on day 1 and maintained at 16.5–18.8°C T\textsubscript{a} (∼61–64 THI) for 1 day of thermoneutral adjustment (Fig. 1). Beginning at 1300 hours on day 2, T\textsubscript{a} was shifted to either 8.4 (∼50 THI) or 32.7°C (∼82 THI) for cold or hot chambers, respectively. These T\textsubscript{a} were achieved at approximately 2400 hours and maintained at a stable level through 1300 hours on day 3. This was followed by a rapid return to thermoneutrality (∼17.0–20.5°C; ∼61–66 THI; Fig. 1). The largest rate of change in T\textsubscript{a} for either chamber was no greater than 1.7°C per hour.

Thermoregulatory measurements were taken at different times to include thermoneutral (i.e., baseline), transition, and stable periods (Fig. 1). Shoulder and rump skin regions were shaved (7 × 7 cm area) 1 day before the start of the experiment to allow for skin temperature (T\textsubscript{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 min period using an infrared thermometer (Model C-1600, Linear Laboratories, Fremont, CA). Rectal temperature (T\textsubscript{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 movements over a 1 min interval.

Sweat rate was determined using a calibrated, digital moisture sensor (Vapometer; Delfin Technologies, Finland) that has been used to determine transepidermal water loss of humans and cattle (Nuuinen et al. 2003; Gebremedhin et al. 2007). All calibrations are certified and performed at the company laboratory using three different relative humidities. Recent studies have used the same type of device to measure moisture loss in a range of situations and environments (Nuuinen et al. 2003). The Vapometer is a closed system approach, free of ambient airflow, and allows for flexible monitoring of cutaneous water loss in laboratory and field environments. Ambient relative humidity and temperature are measured automatically prior to skin application. The device is then held on the skin for 10–20 s before the evaporation rate is displayed in grams per meter squared hour (g m\textsuperscript{-2} h\textsuperscript{-1}). The time between measurements is automatically controlled to allow the relative humidity in the chamber to decrease back to the ambient conditions.
level measured prior to skin contact. Only after this level is achieved will the Vapometer allow the next measurement.

Analysis

Data was analyzed using the two-way repeated-measures ANOVA procedure and standard least squares model fit (JMP; SAS Institute, Cary, NC). Components of the statistical model included chamber, measurement time, and chamber by measurement interactions. When ANOVA revealed a significant difference \((P<0.05)\) in least squares means, a Tukey–Kramer multiple comparisons test (Steele and Torrie 1980) was performed to determine both between- and within-treatment effects. Statements of significance always refer to \(P<0.05\) when not indicated otherwise in parentheses. Multivariable correlation analysis was evaluated using the Fit Line and Fit Polynomial commands (JMP; SAS Institute) estimated by least squares regression to determine linear and quadratic relationships between selected variables.

Results

Rectal temperature (Fig. 2; 38.7 vs 39.0±0.1°C) and respiration rate (Fig. 3; 65 vs 78±6.2 RPM) were not different between test groups during adjustment to the thermoneutral condition \((P>0.08)\). 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 \(T_{\text{skin}}\).

Hot and cold chambers did not differ \((P=0.10)\) for \(T_{\text{skin}}\) during measurement 1 (Fig. 4; 33.5 vs 35.6±0.5°C). Likewise, sweat rates at the two skin sites were not different \((P=0.31)\) at thermoneutrality (shoulder: 40.0 vs 46.0±8.0 g m\(^{-2}\)h\(^{-1}\); rump: 43 vs 52.6±3.0 g m\(^{-2}\)h\(^{-1}\)). These results show that there were no group differences in determinants of thermal status prior to the change in \(T_a\).

The transition period (Measurement 2) for cold and heat exposures exhibited similarities and differences in the magnitude of thermoregulatory response. Neither cold nor heat exposures during the transition period produced a
significant change in $T_{re}$ (Fig. 3). In contrast, $T_{skin}$ significantly decreased ($P<0.05$) by 2°C in the cold (Fig. 4) and increased in the heat (Fig. 4; $P<0.01$) to make it the earliest indicator of transitional change. Respiration rate decreased in the cold by 20 RPM (Fig. 2; $P<0.05$), but increased by only 4 RPM (Fig. 2; $P<0.05$) with heat exposure during the transition period. Likewise, shoulder and rump sweat rates exhibited a significant reduction (20 g m$^{-2}$ h$^{-1}$; $P<0.05$) in the cold, but no change ($P>0.10$) in the heat during transition.

As expected, steady-state exposure to cold and heat conditions (Measurement 4) produced more reliable changes in most indicators of thermal status. Mean $T_{re}$, which is the more traditional indicator, remained stable in the cold (38.7 and 38.5°C, respectively; Fig. 3). In contrast, respiration rate (Fig. 3; 36 and 34 RPM, respectively) and $T_{skin}$ (Fig. 4; 29.6 and 29.2°C, respectively) continued to decrease and were lower ($P<0.05$) from thermoneutral level. Shoulder and rump sweat rates remained low during cold exposure. Mean $T_{re}$ in the heat-exposed group was different from the thermoneutral level (38.9 to 39.1°C; Measurement 1 vs Measurement 3) after 23 h exposure (Fig. 2; $P<0.05$). Respiration rate in Measurement 3 increased by nearly 50 RPM (Fig. 3; $P<0.001$), and was maintained at this level through Measurement 4. Skin temperature remained above thermoneutral level during Measurements 3 (Fig. 4; 35.6 to 37.9°C) and 4 (Fig. 4; 37.9°C). Sweat rates of shoulder and rump sites were very different ($P<0.01$), with the shoulder site increasing more than four-fold above the level at $T_{a}$ 27°C (46.8 to 224.8 g m$^{-2}$ h$^{-1}$), and rump sweat rate showing only a slight increase (51.4 to 59.0 g m$^{-2}$ h$^{-1}$). Like other parameters, shoulder sweat rate peaked during Measurements 3 and 4 (224.8 and 153.6 g m$^{-2}$ h$^{-1}$, respectively; $P<0.001$). Rump sweat rate showed only a slight increase from previous measurements ($P>0.25$).

Nearly all measured values in the cold chamber during Measurement 5 (return to thermoneutrality) were similar to those from Measurement 1 at thermoneutrality. Rump sweat rate, being the exception, was lower from Measurement 1 (27.3 vs 42.9 g m$^{-2}$ h$^{-1}$, $P<0.05$), but not different during the other measurements. Similarly to the cold chamber, the return to thermoneutrality from heat stress in the hot chamber resulted in a re-establishment of thermoneutral values for most variables. Skin temperature, however, was lower during Measurement 5 compared to Measurement 1 (Fig. 4; 32.7 vs 35.6°C; $P<0.05$). As seen during the cold exposure, rump sweat rate following heat stress (33.7 g m$^{-2}$ h$^{-1}$) was below the initial thermoneutral level (52.6 g m$^{-2}$ h$^{-1}$; $P<0.01$).

All measured parameters were evaluated to determine correlation coefficients and predictors of acute heat and cold stress. Mean 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 had a quadratic rather than a linear relationship (Fig. 5a; $r=0.90$ vs 0.94; $P<0.001$). Respiration rate also showed a good correlation with $T_{skin}$ (Fig. 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. 5c; $r=0.60; P<0.01$). Rectal temperature had the

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**Fig. 5** a Respiration rate [respirations per minute (RPM)] plotted as a function of air temperature (°C). Solid line Best fit line. b Sweat rate (g m$^{-2}$ h$^{-1}$) plotted as a function of skin temperature (°C). ● Shoulder skin site, ○ rump skin site, dashed line shoulder best fit line, solid line rump best fit line. c Rectal temperature (°C) plotted as a function of air temperature (°C). Solid line Best fit line
lowest correlation with $T_a$ for all variables, including $T_{\text{skin}}$ (Fig. 6c; curvilinear: $r=0.60$, $P<0.01$; linear: $r=0.36$, $P<0.05$) and respiration rate (Fig. 6a; $r=0.60$, $P<0.01$), to suggest that it is not a good indicator of acute heat or cold stress.

Finally, thermal inputs and thermoregulatory effectors of heat loss were evaluated to determine potential drivers of sudomotor activity. Consistent with the above results, $T_{\text{re}}$ input showed the lowest correlation with sweat rate at both sites (Fig. 6b; shoulder, $r=0.61$, $P<0.001$; rump, $r=0.52$, $P<0.01$). Skin temperature input on the other hand was highly correlated with shoulder ($r=0.86$, $P<0.001$) and rump (Fig. 7b; $r=0.82$, $P<0.001$) sweat rates. Respiration rate was also highly correlated with shoulder ($r=0.93$, $P<0.001$) and rump ($r=0.82$, $P<0.001$) sweat rates. Both respiration rate and $T_{\text{skin}}$ 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. 5b; $r=0.98$, $P<0.001$). The best fit relationship for shoulder sweat rate with $T_{a}$ was a fourth-order polynomial relationship (Table 1). Rump sweat rate, which also exhibited a high correlation (Fig. 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 lag or lack of change in rectal temperature response has been observed during acute heat stress (Lefcourt and Adams 1996), and has been attributed to the effectiveness of physiological heat dissipaters (e.g., respiratory and cutaneous evaporations). Likewise, the lack of change in this parameter in the present study could be attributed to the successful dissipation of body heat during short-term thermal stress. Similarly, the body mass of the cattle in this study provides thermal inertia, which would predictably slow both the increase and decrease in core body temperature and, in effect, result in little change in this 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 chambers, $T_{\text{skin}}$ 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 latter cold stress study using sheep, it was reported that $T_{\text{skin}}$ at the extremities decreased at the rate of 1°C per degree centigrade decrease in $T_a$, suggesting vasoconstriction. However, $T_{\text{skin}}$ at the trunk showed only a marginal decrease. Slee (1968) suggested that $T_{\text{skin}}$ 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 $T_{\text{skin}}$ returned to thermoneutral level, recovery from heat stress decreased $T_{\text{skin}}$ 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; 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 core 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 sweat rate, a less sensitive indicator, responded only to $T_a$ above 25°C. McLean (1963) found a similar result with regards to sweat rate, stating that, at 15°C, the rate of moisture vaporization for all regions was around 10 g m$^{-2}$ h$^{-1}$, with no increase in vaporization until $T_a$ was above 25°C. McDowell et al. (1954) also found that cattle increase sweat production at approximately 25°C, which is consistent with results reported herein. 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 min) to

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<th>Variables</th>
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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.

Discussion in the literature concerning the mechanisms of sweating includes 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. 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. 1961; 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 (i.e., 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 \( T_a \) (8–40°C), the relationship of sweat rate to mean skin temperature was linear, and this relationship remained in effect across seasons. McLean (1963) noted that exposure of cattle to a constant \( T_a \) of 38°C for 3 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 Hou das 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 h). 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, Murray (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

Fig. 8 Regional differences in sweat gland numbers (see Findlay and Yang 1950)
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 $T_{\text{sk}}$ 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.

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