



Bio-thermal responses and heat balance of a hair coat sheep breed raised under an equatorial semi-arid environment



Vinicius de França Carvalho Fonsêca^{a,c,*}, Alex Sandro Campos Maia^a, Edilson Paes Saraiva^d, Cintia Carol de Melo Costa^a, Roberto Gomes da Silva^a, Khalid Ahmed Abdoun^b, Ahmed Abraham Al-Haidary^b, Emad Mohammed Samara^b, Andrea Fuller^c

^a Innovation Group of Biometeorology, Behavior and Animal Welfare (INO BIO-MANERA), Biometeorology Laboratory, São Paulo State University, Jaboticabal, Brazil

^b Department of Animal Production, King Saud University, Riyadh, Saudi Arabia

^c Brain Function Research Group, School of Physiology, University of the Witwatersrand, Johannesburg, South Africa

^d Animal Biometeorology and Ethology Group (BIOET), Federal University of Paraíba, Areia, Brazil

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ABSTRACT

Long-term assessments of bio-thermal responses in a hair coat sheep breed were performed to investigate the effect of the thermal environment on their physiological performance and thermal balance. Twelve healthy non-lactating Morada Nova ewes (3 ± 1.2 years old, body mass 32.7 ± 3.7 kg) were assigned in two 12×12 latin square designs (from 07:00 to 19:00 h and from 19:00 to 07:00 h, respectively) for assessments of their bio-thermal responses during 24 consecutive days. There was a monophasic pattern in the ambient temperature (T_A), which ranged between 21 and 38 °C, thereby exposing the ewes to different levels of surrounding T_A over the day and influencing several of their bio-thermal responses ($P = 0.0001$). Their body temperatures (i.e., rectal, skin, and hair coat surface temperatures) gradually increased ($P = 0.0001$) from 04:00 h. The mean peak for rectal temperature (39.3 °C) was recorded at 19:00 h, while for skin and hair coat surface temperatures it occurred at 13:00 and 14:00 h, respectively. The sensible heat loss by long wave radiation and surface convection exceeded the metabolism of ewes when the T_A was below 24 °C, which usually occurred between 24:00 and 06:00 h. During exposure to higher ambient temperatures, the sheep increased respiratory evaporative heat loss, without panting. In conclusion, the sheep regulated rectal temperature within a relatively narrow range of 1.4 °C over 24 h, and appear to be well adapted to coping with heat. Minimum 24 h body temperature was correlated with minimum T_A , indicating that heat conservation strategies are likely to be important for Morada Nova sheep in a tropical biotype at night, when rates of sensible heat loss exceed the heat generated by metabolism.

1. Introduction

The bioclimatic condition of any semi-arid tropical biotope, such as the majority of the Brazilian regions, can be described as a dry and extremely hot condition with marked fluctuations of water and feed resources (Pfister and Malechek, 1986). In such a biotope, several environmental zeitgebers allow mammals to anticipate seasonal changes through synchronizing their biological clock. The strongest entrainable zeitgeber for mammals is the photoperiod (Weinert and Waterhouse, 2007; Al-Haidary et al., 2016), while other non-photic zeitgebers include the ambient temperature, sleep/wake, and rest/activity cycles, as well as the feeding/drinking pattern (da Silva and Minomo, 1995; Piccione and Caola, 2003; Al-Haidary, 2006). The influence of the ambient temperature cycle produces a signal that affects the

thermoregulatory system in mammals (Pittendrigh, 1993; Maloney et al., 2013; Kaylan et al., 2017). As homeotherms, mammals maintain a state of body thermal homeokinesis at thermoneutrality, and their exposure to supra-neutral conditions forces them to reduce their thermogenic mechanisms and to recruit their thermolytic mechanisms (Renaudeau et al., 2012; Mitchell et al., 2018). Consequently, mammals require appropriate phenotypic traits in order to survive in a semi-arid tropical biotope.

Previous research in arid and semi-arid tropical regions has explicitly demonstrated that small ruminants can endure and inhabit such harsh conditions, as a consequence of several factors. Their relatively small body mass results in a low metabolic requirement (El-Nouty et al., 1988; Samara et al., 2016) and they have skillful grazing behavior, an efficient digestive system, high recycling rate of urea, and thus an

* Corresponding author. Brain Function Research Group, School of Physiology, University of the Witwatersrand, Johannesburg, South Africa.
E-mail address: vinicius.fonseca@wits.ac.za (V. de França Carvalho Fonsêca).

efficient utilization of low nutritive-value forages (Silanikove, 2000; Cain et al., 2006; Fuller et al., 2014). Additionally, these ruminants could possess a heat-resistant genotype, with adaptations that reduce the cost of regulating their body heat balance, ultimately allowing them to maintain a relatively constant body temperature (McManus et al., 2011a; McManus et al., 2011b; Al-Haidary et al., 2012;).

One adaptation that may allow ruminants to reduce heat gain from the environment is a well-insulated coat (Silanikove, 2000; Piccione and Caola, 2003). Ruminants with a less insulated coat surface (e.g., hair coat sheep breeds) may be more vulnerable to daily environmental thermal fluctuations compared to those that are well insulated. The Morada Nova sheep, a hair coat sheep breed raised under an equatorial environment, is important as a genetic and sustainable livelihood resource in Brazil (Egito et al., 2002). To date, we are unaware of any research that has specifically examined the dynamics of heat production and heat loss in a hair coat sheep. In the scenario of high ambient temperature fluctuation, as observed in an equatorial semi-arid environment (Fonsêca et al., 2014), lower insulated animals such as this sheep breed may maintain thermal balance either by preventing rapid body heating during the hottest part of the day, or by storing heat and dissipating it at night. At night, they may need to adopt behaviours, such as huddling, to reduce body heat loss resulting from poor insulation.

In order to determine how these ruminants cope with the thermal conditions imposed by a semi-arid tropical biotope, we assessed their bio-thermal responses to changes in the thermal environment. The majority of the studies investigating the effect of environmental thermal stress on ruminants' thermal regulation have been restricted to measurements taken for short intervals over the day. We designed our experiment to obtain measurements over 24 h, allowing us to determine how the Morada Nova sheep alters heat balance and regulates body temperature over the day.

2. Material and methods

2.1. Location

The present study was carried out at the Small Ruminants Research Center (07° S, 36° W, and 458 m altitude), São João do Cariri, State of Paraíba, Brazil, between March and June of 2015.

2.2. Animals, management, and study design

Twelve healthy non-lactating Morada Nova ewes with a mean live body mass of 32.7 kg (SD = 3.7) and age of 3 years (SD = 1.2) were assigned in two 12 × 12 latin square designs (from 07:00 to 19:00 h and from 19:00 to 07:00 h, respectively) for assessments of their bio-thermal responses during 24 consecutive days. Ewes were collectively housed in a confinement area (13.0 × 7.0 m) with a shelter structure area of 5.0 × 5.0 m. They were maintained throughout the study on the same diet, offered twice daily at 1.5% of their body mass, while water was offered *ad libitum*. During the first latin square design, feed was available at 06:00 and 19:00 h, while feed was offered at 17:00 and 07:00 h in the second latin square design. The diet provided in the present study was a pre-formulated total mixed ration consisting of 85% roughage (*Pennisetum purpureum* hay) and 15% concentrate feed (corn 380 g kg⁻¹, wheat 240 g kg⁻¹, soybean meal 360 g kg⁻¹, and mineral supplement 20 g kg⁻¹), and contained on As-Fed basis; 90% DM; 56 g kg⁻¹CP, and 750 g kg⁻¹NDF.

Before experiments, ewes were first accustomed to the measuring equipment for approximately three months, to decrease their fear to humans, the squeeze chute and face mask. During the data collection period, they were individually placed for 50 min inside a squeeze chute under the shelter structure to obtain their bio-thermal measurements. All procedures described in this study were approved by the Ethics, Bioethics, and Animal Welfare Committee at the São Paulo State

University (Process Number: 17.519/14).

2.3. Study measurements

Meteorological parameters including dry-bulb ambient temperatures (T_A , °C), relative humidity (R_H , %), black globe temperature (T_{GN} , °C), and ambient vapor pressure ($P_P\{T_A\}$, kPa) were all continuously recorded near to the squeeze chute (± 0.5 m) at 1-min intervals throughout the study. T_A and R_H were obtained using a data logger (Model U12–012, Onset; Range = -20 °C– 70 °C for T_A and 5%–95% for R_H ; Accuracy = ± 0.35 °C for T_A and $\pm 2.5\%$ for R_H) mounted at the animal height. The T_{GN} was measured using an external-channel thermistor probe (Model UX120-006M, Onset; Range = -40 °C– 100 °C; Accuracy = ± 0.25 °C) inserted inside a 0.15 m black painted copper sphere placed 50 cm above the ground. The mean radiant temperature (T_{MR} , °C) was thereafter calculated using T_{GN} data according to Da Silva et al. (2010). The $P_P\{T_A\}$ was measured using a water vapor analyzer (Model RH-300, Sable System; Range = 1 kPa–6 kPa; Accuracy = 0.05 kPa), while wind speed was neglected because it was near to zero inside the shade structure for most of the day.

Bio-thermal parameters were obtained using a system developed by our laboratory for evaluation of an animal's thermal status (Maia et al., 2016), and included; proportions of oxygen (O_2 , %) and carbon dioxide (CO_2 , %) in the exhaled air, volumes of oxygen consumed (VO_2 , L h⁻¹) and carbon dioxide output (VCO_2 , L h⁻¹), respiratory quotient (Q_R), respiratory rate (R_R ; breaths·min⁻¹), ventilation rate (V_E , L s⁻¹), saturation pressure of water vapor in the exhaled air ($P_S\{T_{EXP}\}$, kPa), as well as the exhaled air (T_{EXP} , °C), rectal (T_R , °C), skin (T_{EP} , °C), and hair coat surface (T_S , °C) temperatures. Details of the system have been previously described (Maia et al., 2016; Fonsêca et al., 2017; also see the supplementary material). The total rate of metabolic heat production (q^{met}), rates of heat exchange by long-wave radiation (q^{rl}) and surface convection (q^{conv}), as well as the rates of heat lost by sensible avenues (q^{sens}) and respiratory evaporation (q^{er}) were determined using biophysical equations, as described by da Silva and Maia (2013) and earlier reports (Maia et al., 2016; Fonsêca et al., 2017). Note that; (1) all these terms were given as the rate of energy change with time per unit of surface area ($W\cdot m^{-2}$), (2) thermal energy absorbed by short-wave radiation was not considered due to the fact that ewes were protected from direct solar radiation during the assessment, and (3) the diffuse and reflected radiations were assumed to be negligible.

2.4. Statistical analyses

Data were analyzed using the statistical analysis system program (SAS Inst., Inc., Cary NC, USA) using the PROC GLM procedure. The mathematical model was as follows; $y_{ijklmn} = \mu + Q_i + D(Q)_{ij} + H(Q)_{jk} + A_l + T_m + \epsilon_{ijklmn}$, where y_{ijklmn} is the n th observation of the response variables; μ is the overall mean, Q is the random effect of the i th latin square (Q_{L1} and Q_{L2}); $D(Q)$ is the random effect of the j th day of evaluation within the i th Latin square (if $i = Q_{L1}$, then $j = 1, 2 \dots 12$; if $i = Q_{L2}$, then $j = 13, 14 \dots 24$); H is the fixed effect of the j th class of hour within the i th Latin square (if $i = Q_{L1}$, then $k = 07:00, 08:00, \dots, 18:00$, if $i = Q_{L2}$, then $k = 19:00, 20:00, \dots, 06:00$); A is the random effect of the l th animal ($l = A_1, A_2 \dots A_{12}$); T is the fixed effect of the m th class of air temperature ($m = 22, 23, \dots, 37$ °C); ϵ_{ijklmn} is the residual term, including the random error. Statistical means were compared using the least squares method (Harvey, 1960). The probability value that denotes statistical significance was declared at $P < 0.05$. The pairwise comparisons were performed using the Tukey test, and Pearson correlations were conducted between response variables. Furthermore, according to the analysis of the T_A , a principal component analysis was performed to verify any dissimilarity patterns in measured and calculated bio-thermal parameters according to T_A , where 16 classes of T_A were divided into 4 groups under 2 principal components (Z_1 and Z_2).

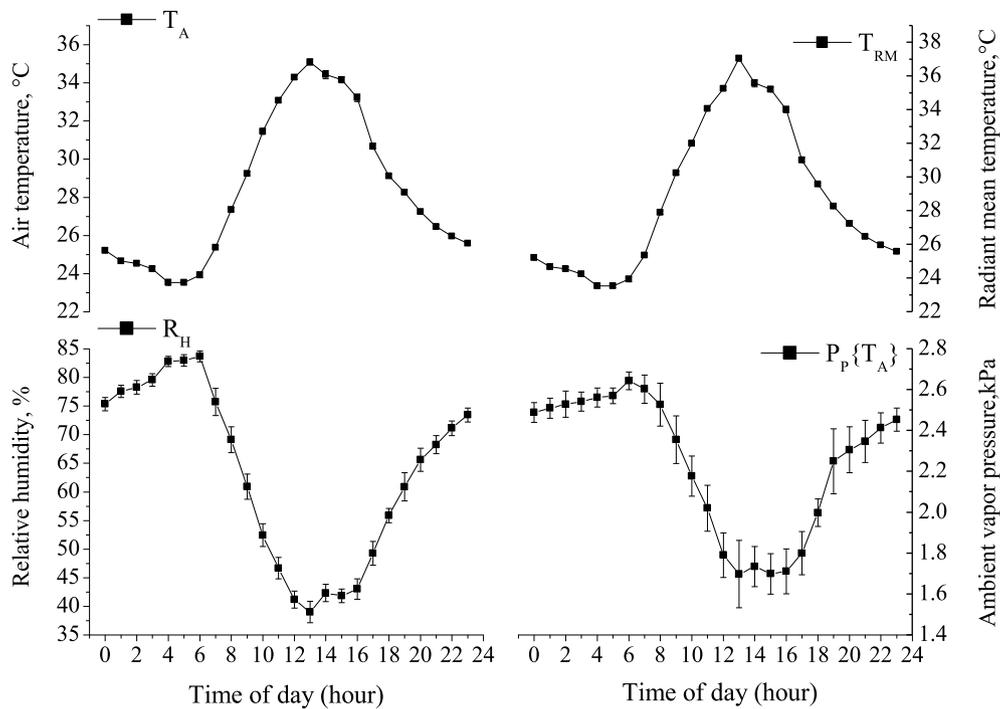


Fig. 1. Least-square means of 1-min interval daily recorded dry-bulb ambient temperatures (T_A , °C), relative humidity (R_H , %), mean radiant temperature (T_{RM} , °C), and ambient vapor pressure ($P_P\{T_A\}$, kPa) throughout the study period. Data are presented as the mean \pm SEM.

3. Results

3.1. Meteorological parameters

The least square means for 1-min interval daily recorded air temperature (T_A) clearly exhibited ($P = 0.0001$) a monophasic pattern throughout the present study (Fig. 1). Analyses of the T_A showed that it had an average of 28.9 °C, with a maximum value of 38.0 °C recorded at 13:00, minimum of 21 °C at 05:00, and a range of oscillation of 17 °C (Table 1). The mean radiant temperature showed ($P = 0.0001$) a similar pattern, while the relative humidity and ambient air vapor pressure showed ($P = 0.0001$) the reverse pattern (Fig. 1).

3.2. Bio-thermal parameters

Least-square means of bio-thermal parameters in Morada Nova ewes are depicted in Figs. 2–4. The volumes of oxygen (VO_2) and carbon dioxide (VCO_2) had respective average values of 6.5 and 7.2 L h⁻¹. The VCO_2 remained greater than VO_2 at night (from 19:00 to 05:00 h), while both parameters interchanged afterward so that VCO_2 was higher than VO_2 from 06:00 to 11:00 h and the opposite was observed from 11:00 to 17:00 h (Fig. 2). Such a pattern resulted in substantial alterations in the calculated respiratory quotient, where it remained stable throughout the night, but increased transiently after feeding. The metabolic heat production had average value of 44.8 \pm 2 W m⁻² and oscillated ($P = 0.0001$) from 35 \pm 2 W m⁻² at 07:00 h to

45 \pm 1 W m⁻² at 17:00 h. Moreover, peaks of metabolism were observed between 07:00 and 08:00 h, and from 15:00 to 18:00 h (Fig. 2).

Body temperatures of ewes gradually increased ($P = 0.0001$) from 04:00 h. The mean peak of rectal temperature (T_R) was recorded at 19:00 h, while for skin (T_{EP}) and hair coat surface (T_S) temperatures it occurred earlier at 13:00 and 14:00, respectively (Fig. 3). The means of rectal temperature oscillated ($P = 0.0001$) from 37.9 \pm 0.2 to 39.3 \pm 0.1 °C. Mean rectal temperature was weekly positively correlated with the ambient air temperature (T_R and T_A , $r = 0.48$, $P = 0.0021$), while maximum 24 h rectal temperature was not correlated with maximum daily air temperature ($r = 0.22$; $P = 0.3384$). However, the minimum 24 h mean of rectal temperature was strongly positively correlated with minimum air temperature levels ($r = 0.80$, $P = 0.0001$). The mean skin temperature oscillated from 34.4 \pm 0.4 to 37.3 \pm 0.1 °C, and hair coat surface temperature from 31.0 \pm 0.2 to 37.6 \pm 0.2 °C. These temperatures were strongly and positively correlated with the ambient air temperature (T_{EP} and T_A , $r = 0.89$, $P = 0.0001$; T_S and T_A , $r = 0.91$, $P = 0.0001$). Heat exchange between ewes and their environment by sensible means (i.e., long wave radiation and surface convection) showed a reverse ($P = 0.0001$) pattern to that of the body temperatures (Fig. 3). Heat loss by sensible avenues progressively decreased ($P = 0.0001$) from 05:00 to 15:00 h, then substantially increased from 15:00 to 05:00 h. Meanwhile, the respiratory rate (R_R), saturation pressure at the exhaled air ($P_S\{T_{EXP}\}$), exhaled air temperature (T_{EXP}), and the rate of evaporative water loss through the respiratory tract (q''_{er}) showed a reverse pattern (Fig. 4).

Based on the principal component analysis, results showed that both of the Z_1 and Z_2 represented 94.87% of the total variance, where Z_1 accounted for 85.60% while Z_2 accounted for only 9.27%. Five bio-thermal responses (i.e., R_R , $P_S\{T_{EXP}\}$, T_{EP} , T_S , and T_{EXP}) were the most relevant parameters as they were highly correlated ($P = 0.0001$) with the Z_1 (Fig. 5). In fact, according to the confirmatory analyses, overall means of skin (T_{EP}), hair coat (T_S), exhaled air temperature (T_{EXP}), respiratory rate (R_R), and saturation pressure at the exhaled air ($P_S\{T_{EXP}\}$) all increased ($P = 0.0001$) as T_A rose (Figs. 5 and 6). Meanwhile, only two parameters (i.e., V_E and T_R) presented weak contributions to separation of groups, as they remained ($P = 0.1100$)

Table 1

Average, minimum and maximum recorded values of air temperature (T_A), relative humidity (R_H), mean radiant temperature (T_{RM}), and ambient vapor pressure ($P_P\{T_A\}$) during the study.

Variable	n	Average	Minimum	Maximum
T_A , °C	2876	28.9	21	38
R_H , %	2880	62.1	27	88
T_{RM} , °C	2804	29.2	21	39
$P_P\{T_A\}$, kPa	2881	2.1	0.9	3.1

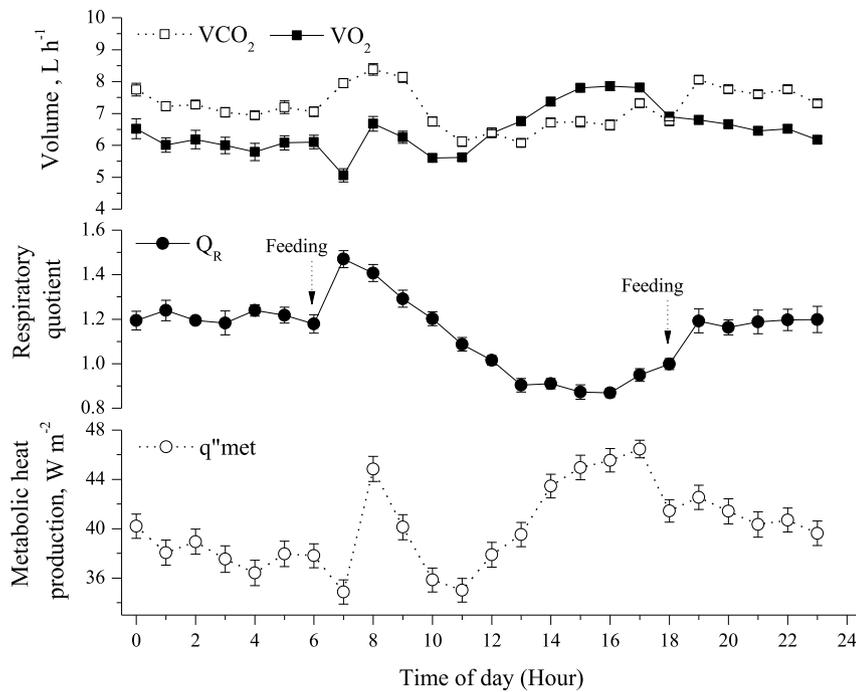


Fig. 2. Least-square means of daily recorded proportions of volumes of oxygen (VO_2 , $L \cdot h^{-1}$) and carbon dioxide (VCO_2 , $L \cdot h^{-1}$), respiratory quotient (Q_R), and total rate of metabolic heat production (q''_{met} , $W \cdot m^{-2}$) in Morada Nova sheep reared under a semi-arid tropical environment. The arrows indicate feeding times. Data are presented as the mean \pm SEM.

relatively stable at all classes of T_A (Figs. 5 and 6). The following values: $T_{EP} = 33.0 \pm 1.0^\circ C$, $T_S = 30.0 \pm 0.4^\circ C$, $T_{EXP} = 26.2 \pm 0.1^\circ C$, and $R_R = 15.2 \pm 0.5 \text{ breaths} \cdot \text{min}^{-1}$ were observed at the lowest T_A class ($22^\circ C$), while the following values: $T_{EP} = 37.7 \pm 0.1^\circ C$, $T_S = 38.3 \pm 0.1^\circ C$, $T_{EXP} = 35.9 \pm 0.3^\circ C$, and $R_R = 26.4 \pm 1.1 \text{ breaths} \cdot \text{min}^{-1}$ were observed at the highest class of T_A ($37^\circ C$). When the metabolic heat production, heat loss by sensible means, and evaporation through respiratory tract of Morada Nova ewes were fitted against T_A classes, the obtained findings showed that metabolism did not ($P = 0.0913$) differ between T_A of 22 and $36^\circ C$ but there was an apparent ($P = 0.0002$) increase at a T_A of $37^\circ C$. The sensible and latent heat losses had noticeable ($P = 0.0001$) changes at this T_A range but in opposite directions (Fig. 7).

4. Discussion

We investigated the bio-thermal responses and thermal balance of a hair-coated sheep, the Morada Nova, exposed to ambient temperature (T_A) that ranged between 21 and $38^\circ C$ (Figs. 1–4). To the best of our knowledge, this is the first study to provide long-term assessments about dynamics of heat balance and bio-thermal parameters with a hair coat sheep breed raised under equatorial semi-arid conditions. The findings revealed that rectal temperature varied, on average, by $1.4^\circ C$, from a minimum at 04:00 h to a maximum at 19:00 h. As air temperature increased, sensible heat loss decreased and respiratory evaporation increased. Although there were two diurnal peaks of metabolic heat production, the metabolism of the sheep appeared relatively stable over a range of ambient air temperatures between 21 and $36^\circ C$.

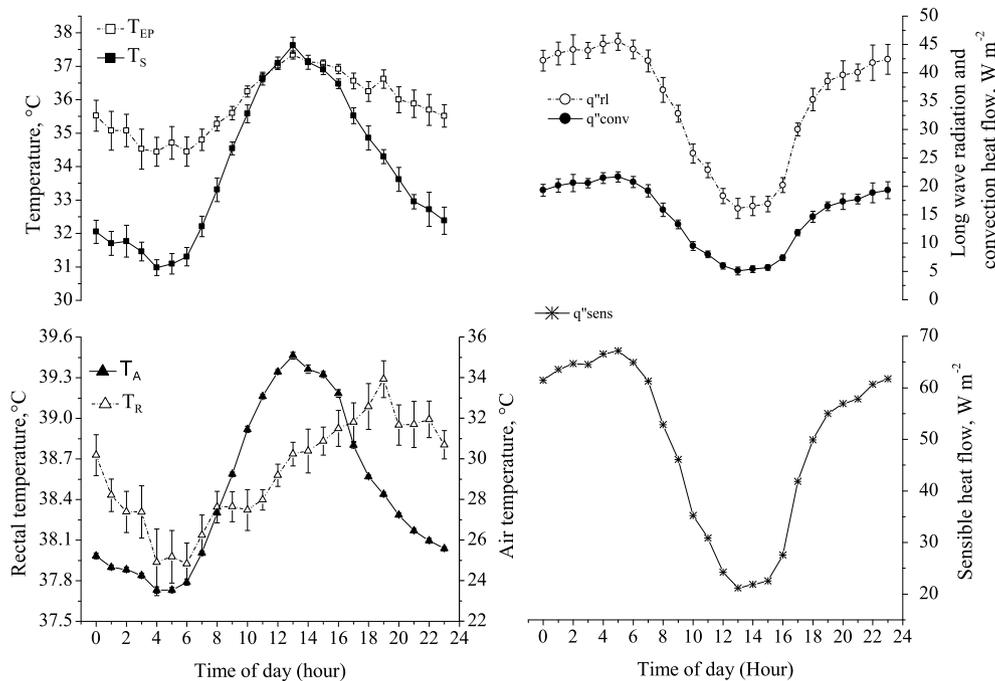


Fig. 3. Least-square means of daily recorded skin (T_{EP} , $^\circ C$), coat (T_S , $^\circ C$), dry-bulb ambient (T_A , $^\circ C$), and rectal (T_R , $^\circ C$) temperatures, as well as rate of heat exchange by long-wave radiation (q''_{rl} , $W \cdot m^{-2}$), surface convection (q''_{conv} , $W \cdot m^{-2}$), and sensible avenues (q''_{sens} , $W \cdot m^{-2}$) in Morada Nova sheep reared under a semi-arid tropical environment. Data are presented as the mean \pm SEM.

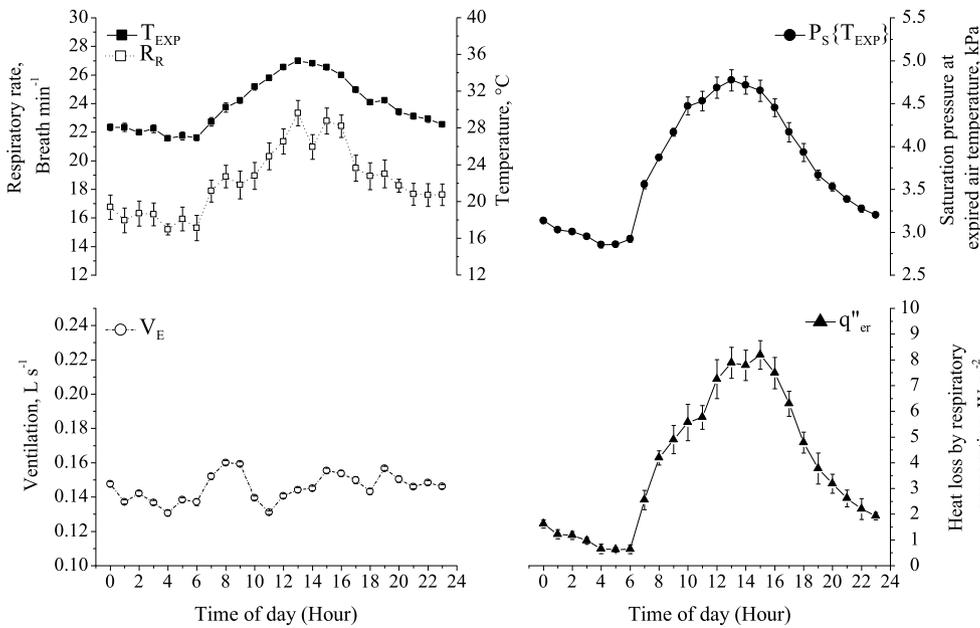


Fig. 4. Least-square means of daily recorded exhaled air temperature (T_{EXP} , °C), respiratory rate (R_R ; breaths·min⁻¹), ventilation rate (V_E , L·s⁻¹), saturation pressure of water vapor in the exhaled air ($P_S\{T_{EXP}\}$, kPa), and the rate of heat lost by respiratory evaporation (q''_{er} , W m⁻²) in Morada Nova sheep reared under a semi-arid tropical environment. Data are presented as the mean ± SEM.

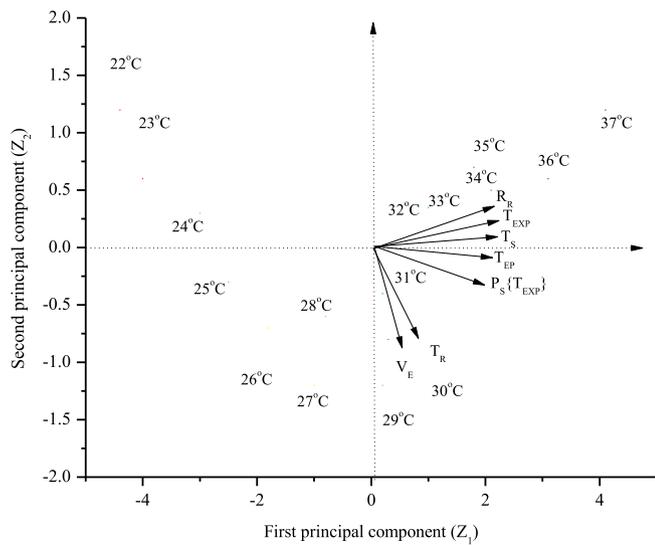


Fig. 5. Consensus configuration by dry-bulb ambient temperatures (T_A) for biothermal parameters analysis. Note that 16 classes of T_A were divided into 4 groups under 2 principal components (Z_1 and Z_2). Parameters defined as; ventilation rate (V_E), respiratory rate (R_R), saturation pressure of water vapor in the exhaled air ($P_S\{T_{EXP}\}$), and temperature of the rectum (T_R), skin (T_{EP}), coat (T_S), and exhaled air (T_{EXP}). Note that correlations (i.e., -1 to 1; represented with arrays) between variables and the principal components (Z_1 and Z_2) were multiplied by a factor of two.

Nocturnally, especially at an ambient air temperature below 24 °C, the thermal gradient between the hair coat surface and air temperature induced rates of sensible heat loss almost twice that generated by metabolism. The minimum 24 h means of rectal temperature were positively correlated with minimum levels of air temperature.

For our study measurements, sheep were restrained and so were not able to implement behavioural thermoregulation, which is likely to be important for them to maintain body temperature when exposed to cool air temperatures at night. The sheep also were not exposed to solar radiation, which is a major factor influencing the thermal balance of free-living animals outdoors (Mitchell et al., 2018). Nevertheless, our analysis of thermal balance in response to a large (17 °C) fluctuation in air temperature revealed that the sheep regulated body temperature

within relatively narrow limits through evaporative and sensible heat loss, without substantial changes in metabolism at the extremes of ambient temperatures. The 24 h pattern of rectal temperature, with a peak in temperature occurring in the evening well after the midday maximum of T_A , is similar to the pattern of body temperature reported for large free-living mammals (Fuller et al., 2016) and other sheep (see below).

The diurnal peaks in metabolism in the early morning and late afternoon were unexpected. However, they occurred soon after feeding and may reflect the influence of excitement associated with feeding and increased metabolism associated with food intake. It is also possible that these peaks of metabolism may be partly attributed to an endogenous pattern associated with the animal's active phase, even though the sheep were restrained. Such a relationship was previously reported in investigations with other herbivore animals (Hendrichs and Hendrichs, 1971). Free-ranging Morada Nova ewes spent the most time grazing from 05:00 to 08:00 h (Fonsêca et al., 2016), and the grazing time budget by a crossbred hair coat sheep was greatest from 06:00 to 09:00 h and from 16:00 to 18:00 h (Morais et al., 2017). Further studies are warranted to clarify the possible relationship between endogenously regulated metabolism and locomotor activity pattern in hair-coated sheep raised in an equatorial semi-arid environment.

The pattern of metabolic rate in a resting mammal can provide a means for researchers to assess how well the animals can tolerate changing environmental temperatures, through determination of the thermoneutral zone. The Commission for Thermal Physiology of the International Union of Physiological Sciences defines the thermoneutral zone to be “The range of ambient temperature at which temperature regulation is achieved only by control of sensible heat loss, i.e., without regulatory changes in metabolic heat production” (IUPS, 1987; 2001). Previous research has shown that the metabolic heat production of a wool sheep breed remained constant across a range of ambient air temperature from 15 to 35 °C, which the authors demarcated as lower and upper limits of the zone of thermoneutrality (Blaxter et al., 1958). For a hair coat sheep breed, Baeta and Souza (1997) reported that the thermoneutral zone had a narrower range, from 20 to 30 °C. In the present study, we found that metabolism of restrained Morada Nova ewes was relatively constant over a 15 °C range of T_A (from 22 to 36 °C; Fig. 7). Despite respiratory evaporation increasing as T_A increased above 22 °C, it occurred with little metabolic cost for the animal. Only at a T_A of 37 °C was an increase in metabolism evident. This finding supports the idea that the energy cost of respiratory evaporative heat loss in sheep is

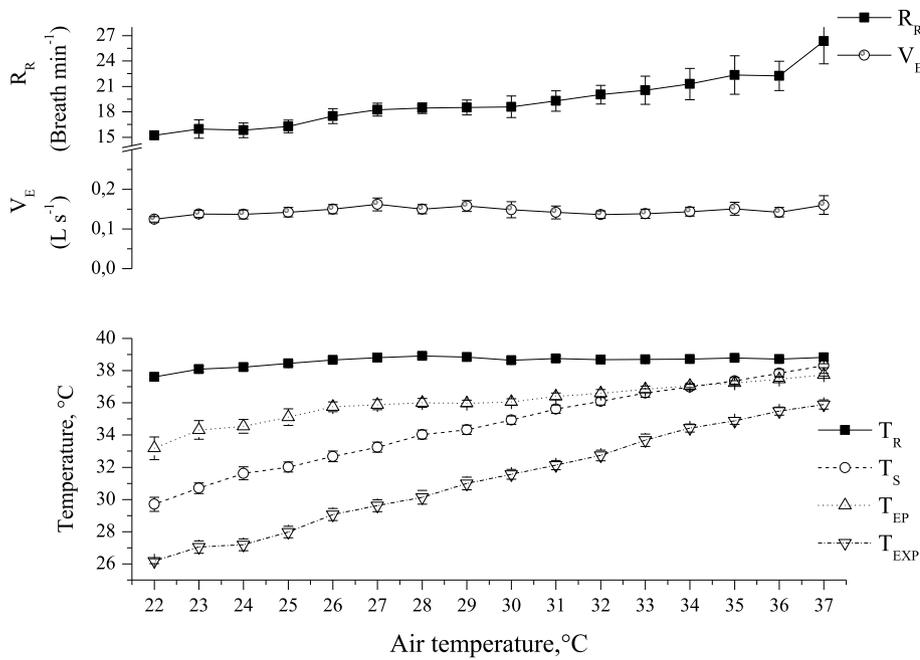


Fig. 6. Thermodiagrams showing the relationship between respiratory rate (R_R ; breaths·min⁻¹), ventilation rate (V_E , L·s⁻¹), rectal (T_R , °C), coat (T_S , °C), skin (T_{EP} , °C), and expired air (T_{EXP} , °C) temperatures as a function of 16 classes of dry-bulb ambient temperatures in Morada Nova sheep reared under a semi-arid tropical environment. Data are presented as the mean \pm SEM.

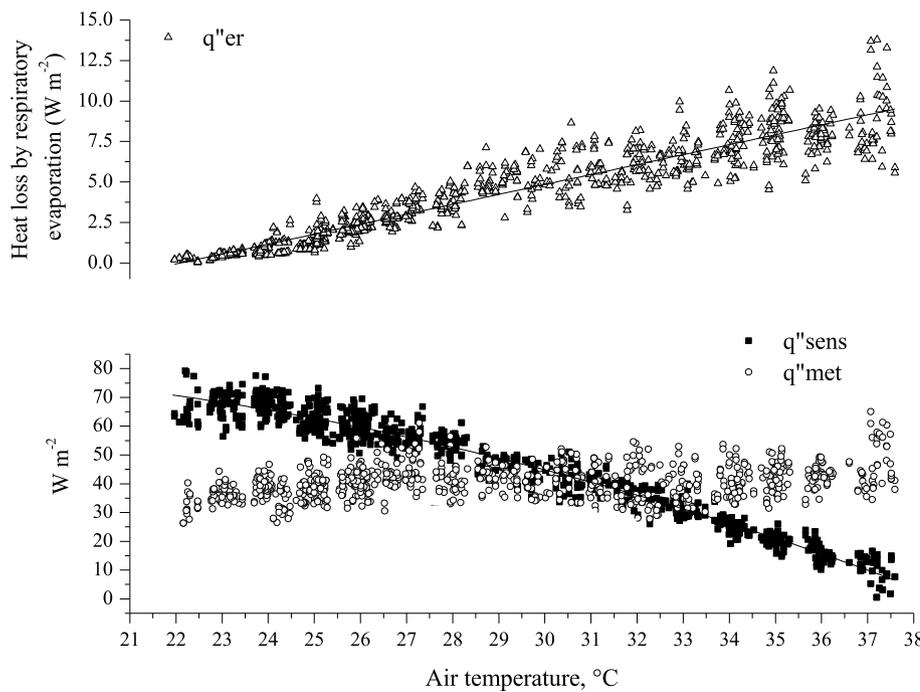


Fig. 7. Thermodiagrams showing the relationship between the total rate of metabolic heat production (q''_{met}), the rate of heat exchange by sensible avenues (q''_{sens} ; surface convection plus long-wave radiation), and heat loss by respiratory evaporation (q''_{er}) as a function of 16 classes of dry-bulb ambient temperatures in Morada Nova sheep reared under a semi-arid tropical environment.

low (Mitchell et al., 2018). Like other large ruminants, hair coat sheep therefore are likely to cope well with heat, so long as they have ready access to drinking water to replace heat lost by evaporation (Fuller et al., 2016).

The absence of an increase in metabolism at lower ambient temperatures, however, may have consequences for maintenance of body temperature in hair coat sheep. We found that the sensible heat loss of hair coat sheep reached almost twice the level of metabolism below a T_A of 24 °C (Fig. 7). Normally, these air temperatures were observed during the night at the same time that rectal temperature reached its lowest value. Over the study period, colder air temperatures at this time of day were associated with lower minimum rectal temperatures. Therefore, we would expect free-living ewes to use strategies to conserve their body heat content at night. Behavioral adjustments to

reduce heat loss, such as huddling, and the possible heat storage throughout the diurnal time could collectively play an important role in avoiding a state of hypothermia nocturnally (Piccione and Caola, 2003). Using an approach suggested by McLean et al. (1983) to determine body heat storage, and considering the maximum recorded ranges for rectal (2.7 °C) and skin temperatures (4.6 °C) between 05:00 and 19:00 h, we find that ewes had a potential to store 5.79 W m⁻² of heat, which represented approximately 14% of the obtained average value for metabolism (Table 2). Finch (1980) documented heat storage around 10 W m⁻² during the diurnal period in black Bedouin goats kept under shade. Huddling behavior has previously been observed in Morada Nova sheep at night (Fonsêca et al., 2019; unpublished data). Such behavior would decrease the exposed surface area and thus reduce heat loss through sensible avenues (Hetem et al., 2009; Collier and

Gebremedhin, 2014; Fuller et al., 2014).

Between a T_A of 28 to 32 °C, on the other hand, the level of heat dissipation through sensible avenues was practically similar to that produced by metabolism (Fig. 7). It is quite well established that T_A affects the oscillations of skin and hair coat surface temperature in sheep (McManus et al., 2009; Piccione et al., 2013; Kaylan et al., 2017) and other animals (Alamer, 2003; Abdoun et al., 2012 Al-Haidary et al., 2016; Samara et al., 2016). Results from the present study revealed that skin and hair coat surface temperature were highly correlated with T_A . The reason for this relationship results mainly from the vasodilatation of the skin capillary bed to subsequently increase peripheral blood flow for heat dissipation through sensible avenues (Piccione et al., 2013; Samara et al., 2014). However, the observed wide amplitudes of skin and hair coat temperatures in the present study were much greater than those reported in previous studies in sheep (Al-Haidary, 2000; Kaylan et al., 2017). This finding might be related to the small body mass, high relative surface area, and the absence of fleece in Morada Nova ewes, which enable this breed to exchange heat much more rapidly than other breeds. Interestingly, Hetem et al. (2009) showed that the circadian variation of skin temperature was more pronounced after shearing in Angora goats assessed under a range of T_A from 10 to 34 °C.

The minimum 24 h levels of rectal temperature were coupled with the lower values of T_A , skin, and hair coat surface temperatures, and high rates of sensible heat loss. However, the calculated correlations were weak (for instance; $r = 0.48$ with T_A). Indeed, the rectal temperature continued to increase until it peaked at 19:00 h, and linearly dropped thereafter. Previous reports have documented a similar pattern for wool sheep raised in a semi-tropical environment (da Silva and Minomo, 1995; Piccione and Caola, 2003; Kaylan et al., 2017), but with lower ranges of oscillation over 24 h. Nevertheless, a 1.4 °C oscillation in rectal temperature of our sheep is much less than that reported for ruminants in some environments (Hetem et al., 2016). In environments with low food or water availability, some mammals show a pattern of heterothermy in their body core temperature (McLean et al., 1983; Ostrowski et al., 2003; Hetem et al., 2016), where they consequently save water by avoiding the excess use of latent avenues and save energy by decreasing the additional increment of thermogenesis.

Above a T_A of 32 °C, sensible avenues were evidently insufficient to dissipate all heat generated by metabolic processes. Latent heat loss gains a progressive importance in dissipating excess body heat content with increasing environmental heat load (Costa et al. 2014). Evaporative heat loss from the respiratory tract of Morada Nova ewes was increased with rises of respiratory rate, expired air temperature, and saturation pressure at the exhaled air. However, the thermal load observed in this study didn't evoke panting in animals, with respiratory rate oscillating only between 15 ± 1 and 24 ± 2 breaths min^{-1} . According to Hemingway and Hemingway (1966) the pattern of respiratory rate of an adult sheep maintained in a thermoneutral environment has been found to be 15 to 25 breaths min^{-1} . On the other hand, over a similar range of air temperature, Corriedale ewes substantially increased their respiratory rate from 35 to 110 breaths min^{-1} (Marai et al., 2007).

In quantitative terms, the latent heat dissipated through the respiratory tract amounted to 18% of the calculated metabolism of ewes in the present study at a T_A of 35 °C, while heat loss by sensible routes contributed to around 50% (Fig. 7). In agreement with these findings, sheep dissipated approximately 20% of their total body heat via respiratory moisture at a T_A of 35 °C (Thompson, 1985). Besides the respiratory tract, heat loss through cutaneous evaporation likely also contributed to body thermal regulation of Morada Nova ewes. Several studies have confirmed that skin temperature is the primary driver for sweating (Maia et al., 2005; da Silva and Maia, 2011). Cutaneous evaporation was not quantified in the present study, but results demonstrated that skin temperature was highly correlated with T_A ($r = 0.89$), and the thin coat is likely to facilitate cutaneous water loss. Therefore, the amount of heat loss through cutaneous evaporation has a

potential to represent around 30% of metabolism at a T_A of 35 °C.

5. Conclusions

The present study sheds some light on how the dynamics of heat production and heat loss dictate physiological adjustments, and how a hair-coat sheep breed copes with the thermal condition imposed under the equatorial semi-arid environment. The sheep coped well at high air temperatures, primarily by increasing evaporative heat loss without an apparent increase in metabolism. The sheep appeared to be more sensitive to cold, with heat loss exceeding metabolism even at a relatively moderate air temperature of 24 °C. Understanding further how Morada Nova sheep cope with changes in the thermal environment requires measurements in free-living animals that are able to implement behavioural thermoregulation, such as huddling and seeking more suitable microclimates. Further research dealing with these aspects may very well improve our understanding about the production, management requirements, and welfare of heat-tolerant sheep raised under harsh environmental conditions.

Compliance with ethical standards

All procedures described in this study were approved by the Ethics, Bioethics, and Animal Welfare Committee at the São Paulo State University (Process Number: 17.519/14).

Conflicts of interest

We declare that no competing interests exist that are of influence on this work.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jtherbio.2019.05.024>.

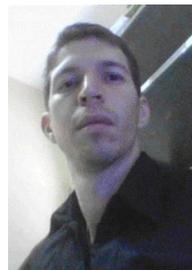
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Vinícius F. C. Fonsêca is a D.Sc. in Animal Science - Federal University of Paraíba - Brazil. He is doing a post-doc in the Innovation Group of Animal Biometeorology, Behavior, and Animal Welfare (INOBIO-MANERA) at the Sao Paulo State University - Brazil. Presently, he has developed research activities with the Brain Function Research Group (BFRG) at the School of Physiology, Wits University - South Africa. His research interest included investigations on the animal behavior and welfare, evaluation of the thermal equilibrium, methods to study heat and mass transfer process in livestock under field, and thermal environmental management.



Alex Sandro Campos Maia received his undergraduate degree in agronomy engineering in 2000 from the Federal University of Acre (UFAC). He received his doctorate in Animal Science from São Paulo State University (UNESP) where he currently teaches animal biometeorology. He is a director Innovation Group of Animal Biometeorology, Behavior, and Animal Welfare (INOBIO-MANERA) at the Sao Paulo State University - Brazil. His interests include animal bioenergetics, thermal mathematical modelling, thermal balance, development of devices to evaluate the thermal equilibrium of Livestock under field.



Edilson Paes Saraiva Graduation, Master's and Doctorate in Animal Science by the Federal University of Viçosa. Professor, Department of Animal Science, Federal University of Paraíba. Coordinator of the research group on Bioclimatology, Ethology and Animal Welfare.



Cíntia Carol de Melo Costa is a D.Sc. in Animal Science - Sao Paulo State University (UNESP), Jaboticabal, São Paulo, Brazil. She is doing a post-doc in the Innovation Group of Animal Biometeorology, Behavior, and Animal Welfare (INO-BIO-MANERA) at the Sao Paulo State University - Brazil. His research interest included investigations on the thermoregulation of beef cattle in tropical environments.



Roberto Gomes da Silva is an Emeritus researcher at the Innovation Group of Animal Biometeorology (INO-BIO-MANERA) at the Sao Paulo State University - Brazil. He has experience in the area of Animal Science, with emphasis on Domestic Animal Ecology and Ethology, working mainly in the following subjects: Physics and Physiology of thermoregulation, pelage, genetics, cattle, sheep and tropical environment.



Khalid Abdoun Khalid Abdoun (ORCID ID: 0000-0003-1208-8903) is a professor at the King Saud University. He earned his PhD in Veterinary Physiology from the Free University of Berlin, Berlin, Germany in 2001. He has been awarded Alexander von Humboldt Postdoctoral Research Fellowship during the period 2005-2007. His research interest is nutritional and environmental physiology. His current research projects focus on suitable nutritional and environmental approaches to mitigate the adverse effects of heat stress and promote production performance of farm animals raised under semi-arid environments. He is actively participated in many international scientific and published more than 60 research and review articles in well reputed international journals.



Ahmed Abraham Al-Haidary Ahmed Al-Haidary (ORCID ID: 0000-0002-4986-4710) is a professor at the King Saud University. He is the head of the biometeorological group in the Department of Animal Production. He earned his PhD degree in Environmental Physiology from the University of Missouri-Columbia, Missouri, United States in 1995. He published more than 100 articles in several peer-reviewed international scientific research journals and conferences. His research focuses on comprehending the environmental problems that hinder or enhance animal comfort and productivity. His research interests include animal-environment interrelationships, animal adaptation, biometeorology, thermophysiology, bioenergetic, biologgging, biotelemetry, circadian rhythms, infrared thermography, manipulating and ameliorating the external environment.



Dr. Emad M. Samara Emad Samara (ORCID ID: 0000-0002-3231-9193) is a veterinarian and faculty animal biometeorologists at the King Saud University. His current research is centered on providing an up-to-date knowledge regarding the basic controlling strategies, tactics and mechanisms of body thermoregulatory system as well as bioenergetics in animals particularly dromedary camels. His research interests include the spatiotemporal modelling of heat transfer, biotelemetry, electrophysiology, molecular thermotolerance, epigenetic adaptation, phenology, neuroethology, paleoclimatology, ergonomics, development of non-living models, as well as innovative non-invasive methodologies. He published more than 50 research articles in several peer-reviewed international scientific research journals and conferences.



Andrea Fuller is Director of the Brain Function Research Group and an Associate Professor in the School of Physiology. The main focus of her current research is the physiological capacity of terrestrial mammals to cope with predicted effects of climate change. Her research interests also include game capture physiology and pharmacology, and the relationship between brain and body temperature regulation in mammals. She is an Executive Committee member of The Section on Thermal Physiology, International Union of Physiological Sciences, and a founding member of the South African Young Academy of Science.