



Identifying potential thermal drivers of sudomotor in camels (*Camelus dromedarius*)



Emad M. Samara^{a,*}, Khalid A. Abdoun^a, Aly B. Okab^{a,b}, Mohammed A. Al-Badwi^{a,c}, Ahmed A. Al-Haidary^a

^a Department of Animal Production, College of Food and Agriculture Sciences, King Saud University, Riyadh, 11451, Saudi Arabia

^b Department of Environmental Studies, Institute of Graduate Studies and Research, Alexandria University, Alexandria, 21526, Egypt

^c Department of Animal Production, Faculty of Agriculture, Ibb University, Ibb, 70270, Yemen

ARTICLE INFO

Keywords:

Thermoregulation · perspiration · sweating · circadian · drivers

ABSTRACT

The mechanism of sudomotor regulation in the family *Camelidae*, as in other mammals, is poorly understood. Five healthy dromedary bulls (400 kg and 4 years-old) were used to examine the interrelationship of sweating rate (SR) with ten thermal parameters measured (and/or estimated) every 3-hr for a 24-hr time period under natural and shaded environmental conditions, in order to subsequently identify the potential thermal drivers of sudomotor in this species. Results revealed that all parameters, including SR, had clearly ($P < 0.001$) exhibited monophasic circadian rhythms. Moreover, the obtained findings pointed out that strong/moderate positive correlations were existed between SR and eight parameters [i.e. ambient (T_a), rectal (T_r), body (T_b), skin (T_{sk}), coat (T_{ct}) temperatures as well as total (ambient-to-body, BTG_t), external (ambient-to-skin, BTG_{ex}), and internal (skin-to-body, BTG_{in}) body thermal gradients] suggesting that they may all be good indicators of sweating activity. Nonetheless, out of those highly-correlated parameters, merely six (i.e. T_a , T_b , T_{sk} , T_{ct} , BTG_t , and BTG_{ex}) showed superior coefficients of determination ($R^2 \geq 0.90$; $P < 0.000$) when interrelated with SR; thereby, implying that they have the potential to drive sudomotor. Notably, however, results were more probably allude that sudomotor is regulated through BTG_t . Accordingly, the onset of sweating (i.e. threshold) and its effective level was determined using BTG_t . A method of how SR can be regulated through BTG_t was proposed according to Webb's theory of controlling body-heat content. Some shortcomings prevent confirming that BTG_t is the best thermal driver of sudomotor in this species were noted. Research dealing with this interesting physiological process requires further experimentation to fully elucidate the basic functional mechanisms of *Camelidae*'s thermoregulatory system.

1. Introduction

Homeothermic bodies can be described as an open thermodynamic system that continuously exchanges thermal energy with their external surrounding (da Silva and Maia, 2013). Under natural conditions, they must dissipate the heat gained from their surrounding together with their own metabolic heat production to maintain a constant body temperature. In fact, body heat dissipation can be enhanced through the external shift of blood distribution (i.e. Newtonian means) and/or by the recruitment of evaporative means, where water is evaporated from the skin and/or respiratory tract (Richards, 1973; Willmer et al., 2000). Of the two basic requirements for evaporation (i.e. water and air movement), sweating animals controls the amount of water, while panting animals controls the amount of air movement (Bianca, 1968).

Camelus dromedarius, as other *Camelidae*, are not known to pant (Allen and Bligh, 1969; Schmidt-Nielsen et al., 1981). It was actually documented that heat dissipation through their respiratory tracts constitutes only 3% of their total evaporative heat dissipation (Schroter et al., 1987). Likewise, Rosenmann and Morrison (1963) concluded from their experiments that panting in *Lama guanicoe* (a relative species) merely occurs under work (e.g. running) and not under heat exposure. In fact, in a later experiment by de Lamo et al. (2001), *Lama guanicoe* did not change their respiratory rate when exposed to ambient temperatures between 20 and 30 °C. Beside that, data from our lab showed that perspiration in *Camelus dromedarius* increased about 10-folds when the effective ambient temperature increased from 10 to 44 °C, with no noticeable changes in their respiratory rates (unpublished observations). This collectively signifies that *Camelus*

* Corresponding author.

E-mail address: Dremas@ksu.edu.sa (E.M. Samara).

<https://doi.org/10.1016/j.jtherbio.2019.102413>

Received 15 April 2019; Received in revised form 4 September 2019; Accepted 9 September 2019

Available online 11 September 2019

0306-4565/ © 2019 Elsevier Ltd. All rights reserved.

dromedarius is mainly a sweating species.

Nevertheless, the mechanism of sweat stimulation (i.e. sudomotor) in the family *Camelidae*, as in other mammals, is poorly understood. This entirely stems from the fact that thermal as well as non-thermal drivers, modulators, and disrupters of sudomotor are still controversial. As a matter of fact, several experiments reported that major differences in sweating rate were unrelated to the internal body temperature. External/ambient temperature was found to be the best thermal driver of sudomotor in mammals, while relative humidity was found to be the main external disrupter under extreme hot conditions (Murray, 1966; Scharf, 2008; da Silva and Maia, 2011). On the other hand, other experiments suggested that skin temperature is the major thermal driver controlling sudomotor (Whittow, 1962; Hammel, 1968). However, because sudomotor was partly delayed despite the elevated skin temperature under extreme hot conditions, researchers implied that central body temperature is the main driver of sudomotor, while skin temperature act only as modulators of the central control signals (Schleger and Turner, 1965; Finch et al., 1982; Samara, 2019). Indeed, Colin and Houdas (1965) proposed that the mechanism of sudomotor for non-adapted animals is centrally activated, whereas in adapted animals the mean skin temperature are able to activate perspiration before the central control send its impulses for heat dissipation. On the contrary, both of the central and peripheral thermoreceptors can provide afferent input to the hypothalamus from which the resultant effectors signals are initiated, according to Berman (1971).

Obviously, further experiments are required to clarify our understanding of how sudomotor is regulated in the family *Camelidae*. Indeed, it is neither clear what are the potential thermal and/or non-thermal drivers, modulators, and disrupters of sudomotor in this family nor how this would be accomplished. The intention of the present experiment was, subsequently, twofold; to first examine the relationship of sweating rate (SR) with several thermal measurements and estimates, in order to identify, as a second objective, the potential thermal drivers of sudomotor in *Camelus dromedarius*.

2. Materials and methods

Five healthy dromedary bulls of a native breed (*Majaheim*, black coat-hair) with a mean live body mass of 400 kg (SD > 24) and age of 4 years (SD < 1.50), were used to conduct this experiment at an experimental station (+24°48' N, +46°31' E) affiliated to the Department of Animal Production, College of Food and Agriculture Sciences, King Saud University. Throughout the experiment, bulls were individually housed in shaded pens (4 × 5 m in size), and maintained on unchopped grass hay Rhodes (*Chloris gayana* spp.) that offered twice daily (06:00 & 17:00 h) at 75 Kcal per kg^{0.75} metabolizable energy per day in agreement with feeding recommendations of Zine-Filali and Guerouali (1994), while they all had free access to a clean tap water and mineral salt.

Under natural environmental conditions, several measurements were determined every 3-hrs (starting at 0:00 o'clock) for a 24-hrs time period (i.e. one day). Dry-bulb ambient temperatures (T_a) and relative humidity (RH) were both continuously recorded every 30-mins using two data loggers (Hobo Pro-Series data logger, model H08-032-08, OnsetComp., Cape Cod, MA, USA) mounted at 2-m from the ground, and placed away from direct sources of heat, sunlight and water. A special data logging software (Box-Car Pro 4, OnsetComp, USA) was utilized for programming these loggers as well as for data retrieving.

In addition, a calibrated digital thermometer (ARTSANA, Grandate CO, Italy) was used to determine the rectal temperature (T_r), while all bulls were surgically fitted with an assembling (thermistor/data logger) to record their tympanic membrane temperature (T_{ty}) as previously described in Samara et al. (2011). Thermistors (27-10K4A80I, Onset Computer Corporation, Pocasset, USA) with 10 K and green insulation were used for temperature sensing, while data loggers (HOB0-U12, Onset Computer Corporation, Pocasset, USA) with a dimension of

75 × 60 × 20 mm and a weight of 50 g had received a lead from these thermistors to store temperature data. Both of the T_r thermometer and T_{ty} thermistors were calibrated against a high-accuracy mercury thermometer by immersing in a water bath during a variable temperature range (35 > 43 °C) for 4-hrs. Temperature resolution of the T_r thermometer and T_{ty} thermistors was proven to have an accuracy of 0.10 °C and 0.04 °C, respectively between readings.

Moreover, an infrared thermometer (Traceable Mini-IR™ Thermometer, Friendswood, TX, USA) with a temperature range of -22 to 110 °C, a resolution of 0.10 °C, an accuracy of ± 1.00 °C (between 15 and 40.0 °C), and an emissivity fixed at 0.95 was used to measure both of the skin temperature (T_{sk}) and coat temperature (T_{ct}). In fact, T_{sk} was measured in two regions (2 × 2 cm in size, at right shoulder and hip) shaved at 24-hrs prior to the experiment commencement, while T_{ct} was measured from fixed sites adjacent to those regions. However, it should be noted that the obtained data of T_{sk} and T_{ct} from both regions were thereafter averaged before analysis to end up with one reading for each camel at every collecting time period.

Using the obtained reading of T_r , T_{ty} and T_{sk} , mean body temperature (T_b) was estimated according to McLean et al. (1982, 1983). In fact, changes in these temperatures were related by the equation: $[\Delta T_b = \alpha \Delta T_r + (1-\alpha) \Delta T_{sk}]$, where the value of α was found in our case herein to be 0.87 (SE < 0.03). Additionally, the formulas; $[T_a - T_b]$, $[T_a - T_{sk}]$, and $[T_{sk} - T_b]$ were utilized to estimate the total (BTG_t), external (BTG_{ex}), and internal (BTG_{in}) body thermal gradients, respectively (da Silva and Maia, 2013).

On the other hand, SR was determined using the cobalt chloride method proposed by Schleger and Turner (1965) and modified by Pereira et al. (2010) at the exact shaved regions used for T_{sk} measurement. In brief, several filter papers were impregnated with 10% of cobalt chloride solution and then prepared as described by Schleger and Turner (1965), while a device was built as noted by Pereira et al. (2010). Thereafter, two (2 × 2 cm) strips of Velcro were glued on the animal surface and to the free ends of Pereira's device. Three cobalt chloride discs were mounted on a double face adhesive strip fixed on the device immediately prior to be placed on the animal surface. The mean time taken by all of the three discs to change their color from blue to pink was recorded with a stopwatch. Subsequently, SR ($\text{g} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$) was calculated using a formula given by Schleger and Turner (1965).

Measured and estimated data were analyzed using the statistical analysis system software (SAS v9.1, SAS Inst., Inc., Cary NC, USA). The PROC MEANS procedure was first used to obtain the descriptive statistics. Then, a completely randomized design was used to analyze the differences in these parameters by the time of day using the PROC GLM procedure, where the model included the fixed effect of the time and the random effect of the animal. Data were thereafter subjected to ANOVA, and mean differences were elaborated by the PDIF option. The probability value that denotes statistical significance was declared at $P < 0.05$. Furthermore, interrelationships among all parameters were attained using the PROC CORR and REG procedures. A principal component analysis (PCA) was thereafter performed to verify any dissimilarity patterns in these parameters according to SR under 2 principal components (PC_1 and PC_2) using the SigmaPlot software (SigmaPlot v12.0, Systat Software Inc., San Jose CA, USA), while the biplot was drawn using Origin software (Origin, 2019b; OriginLab Corporation, Northampton, MA, USA). Considering the experimental data, it is worth mentioning that we used two datasets. The "Whole-dataset" consisted of the entire collected data for each measured/estimated thermal parameter from each camel at each time period, while the "Average-dataset" was built using the mean data of each parameter from all camels at each time period. However, data discussion and conclusions were completely based on analyzing the "Whole-dataset", while "Average-dataset" was merely used herein for presentation.

Table 1
Descriptive analysis of all measured and estimated thermal parameters.

Thermal parameters ^a	Descriptive analysis							
	Mean	Min	Max	SD	SE	CV	Skewness	Kurtosis
Ambient temperature (T_a)	35.34	23.63	48.49	6.86	1.40	19.43	0.14	-1.04
Relative humidity (RH)	10.98	3.90	25.30	5.37	1.10	49.04	1.20	0.85
Tympanic temperature (T_{ty})	38.43	37.80	38.90	0.27	0.06	0.71	-0.44	-0.95
Rectal temperature (T_r)	38.03	37.70	38.50	0.28	0.05	0.70	0.35	-1.18
Skin temperature (T_{sk})	35.92	33.55	37.50	1.07	0.22	2.97	-1.03	0.83
Coat temperature (T_{ct})	35.96	32.35	39.50	1.89	0.39	5.27	-0.05	-0.42
Body temperature (T_b)	37.79	37.33	38.26	0.29	0.06	0.78	0.28	-1.22
Sweating rate (SR)	86.39	19.64	154.96	35.44	7.23	41.03	-0.29	-0.03
Total body thermal gradient (BTG_t)	-2.44	-12.40	8.11	6.60	1.35	-267.23	0.14	-1.02
External body thermal gradient (BTG_{ex})	-0.57	-8.71	9.41	6.02	1.23	-1000.90	0.26	-1.14
Internal body thermal gradient (BTG_{in})	-1.87	-3.80	-0.57	0.88	0.18	-46.85	-1.09	0.78

^a Details are shown in the text.

3. Results

The descriptive analysis of all tested thermal parameters is presented in Table 1. Results showed that all parameters were normally distributed albeit the obtained high CV in few parameters.

Analysis of T_a showed that it ($P < 0.001$) exhibited monophasic circadian rhythm as influenced by the time of day. Despite being measured away from direct sources of heat, sunlight and water, it had a mesor value of 35.34 °C (SE = 1.40), an acrophase at 12:00 h with a zenith value of 48.49 °C, a trough at 06:00 h with a nadir value of 23.63 °C, an amplitude of 13.16 °C, and an oscillation of 24.86 °C (Fig. 1, A). Meanwhile, the educed rhythm of RH ($P < 0.001$) showed the reverse pattern (Fig. 1, B). This was actually a requirement for this experiment, where bulls ought to efficiently undergo a different level of surrounding T_a/RH throughout the day; thus, tangible changes in other parameters may/may not be consequently induced.

As a matter of fact, results revealed that the overall means of all tested parameters, including SR , had clearly ($P < 0.001$) exhibited monophasic circadian rhythms as influenced by the time of day, where nadir values were appeared around 06:00 and zenith values were attained during the 12:00–18:00 time period. These changes are actually depicted in Fig. 1. With a mesor value of 86.39 g m⁻² h⁻¹ (SE = 7.23), the educed rhythm of SR in dromedary bulls was abruptly increased from a nadir value of 19.64 g m⁻² h⁻¹ at the morning (06:00 h) to a zenith value of 154.96 g m⁻² h⁻¹ at middle of the day (12:00 h) (Fig. 1, F). Regarding body thermal gradients, on the other hand, their educed rhythms followed the same pattern as T_a with the exception of BTG_{in} , which remained relatively constant throughout the day (Fig. 1, E).

All parameters were used, thereafter, to determine their correlation coefficients (r) with both of T_a and SR (Table 2). Results demonstrated positive r between T_a and all parameters with the obvious exception of RH . Likewise, it was evident that T_a ($P < 0.000$), T_{ct} ($P < 0.000$), T_b ($P < 0.000$), BTG_t ($P < 0.000$) and BTG_{ex} ($P < 0.000$) had all exhibited strong positive r with SR , while both of T_r ($P < 0.000$) and T_{sk} ($P < 0.000$) had high positive r , BTG_{in} ($P < 0.002$) had moderate positive r , T_{ty} ($P < 0.146$) had weak positive r , while RH ($P < 0.000$) had high negative r with SR (Table 2).

Accordingly, linear relationships of SR versus highly correlated thermal parameters were subsequently applied to identify the potential thermal drivers of sudomotor in *Camelus dromedarius* (Table 3, Fig. 2). The obtained findings pointed out that the best fit ($R^2 \geq 0.80$; $P < 0.001$) linear relationships of SR were versus all parameter except T_r , T_{sk} , and BTG_{in} . Notably, however, only six parameters (i.e. T_a , T_{ct} , T_{sk} , T_b , BTG_t , and BTG_{ex}) were the most relevant parameters based on the PCA, as they were strongly correlated ($R^2 \geq 0.90$; $P < 0.000$) with the PC₁ (Fig. 3).

4. Discussion

For the purpose of identifying the potential thermal drivers of sudomotor in *Camelus dromedarius*, SR and other ten thermal parameters were first measured/estimated, and then the acquired data were examined for interrelationship analyses. Out of these ten parameters, two parameters yielded weak positive and strong negative correlation coefficients with SR (i.e. T_{ty} and RH , respectively), which suggest the inadequacy of these parameters to act as drivers of sweat response in this species. In fact, the level of surrounding RH acts actually as a disruptor of sudomotor, where it previously known that under extreme hot conditions the total heat dissipation through evaporative means is markedly reduced when RH is high (Curtis, 1983; da Silva and Maia, 2013).

On the contrary, the attained strong/moderate positive correlations of SR with other parameters (i.e. T_a , T_r , T_b , T_{sk} , T_{ct} , BTG_t , BTG_{ex} , and BTG_{in}) suggested that they may all be good indicators of sweating activity in camels especially when these finding come in consistent with previous reports on other mammals (Whittow, 1962; McLean, 1963; Schleger and Turner, 1965; Allen and Bligh, 1969; Montalvo and Cevallos, 1973; Finch et al., 1982; de Lamo et al., 2001; Scharf et al., 2008). Out of these highly-correlated parameters, only six (i.e. T_a , T_b , T_{sk} , T_{ct} , BTG_t , and BTG_{ex}) showed superior coefficients of determination ($R^2 \geq 0.90$; $P < 0.000$) when interrelated with SR ; thereby, implying that those parameters have the potential to drive sudomotor. Nonetheless, it remains unclear which one is the most pertinent input or, more realistically, what are the combinations of inputs that collectively drive sudomotor in this species.

The influence of the T_a cycle (as a true synchronizing zeitgeber) on mammals are well-documented, where the reviewed data and information by various researchers have clearly and repeatedly demonstrated that such cue is one of the main environmental factors that evoked circadian rhythmicity in a wide range of physiological and behavioral functions (da Silva and Maia, 2013; Maloney et al., 2013; Kaylan et al., 2017). Actually, it's well known that a rise in the level of surrounding T_a raises SR to a new and steady rate (Murray, 1966; Allen and Bligh, 1969; Yoshida et al., 1995; Scharf et al., 2008). Realistically, however, T_a alone cannot be directly responsible for sudomotor since it must be translated at the receptor level to produce the proposed effect. Likewise, T_{ct} should be ignored due to the fact that it essentially reflects the variations in the surrounding T_a (or more precisely the external radiant exchange) and not the actual variation of the internal body thermal status (Walsberg, 1983; Sejian et al., 2012).

According to the core-shell principle (Curtis, 1983; Baumgard and Rhoads, 2012), on the other hand, the shell ($\sim T_{sk}$) acts as a heterothermic thermal buffer protecting the homeothermic core ($\sim T_r$) from large changes in the surroundings temperature ($\sim T_a$). Thus, under thermoneutral conditions, T_r is usually warmer (higher) than the T_{sk} ,

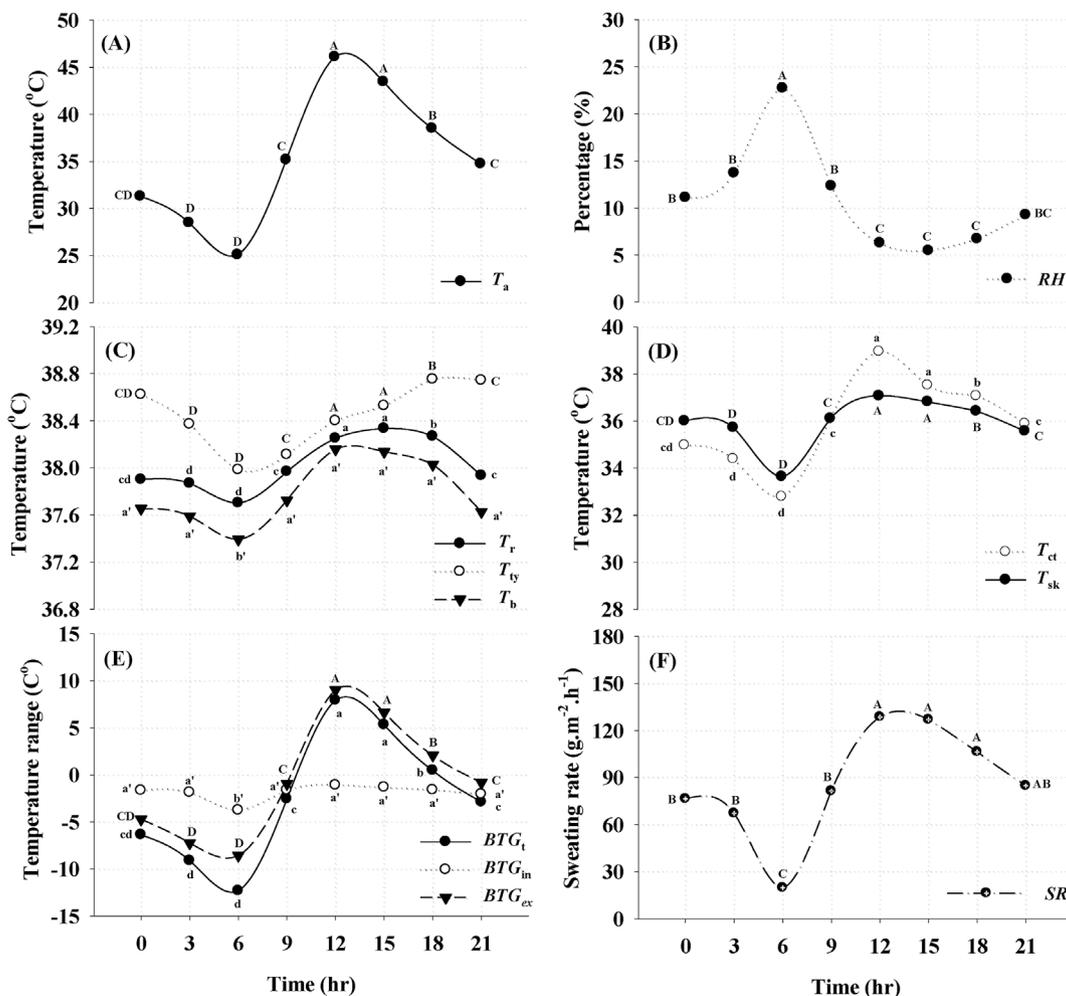


Fig. 1. Daily variations of all tested thermal parameters in dromedary camels reared under natural/shaded environment. Parameter defines as; dry-bulb ambient (T_a), rectal (T_r), tympanic membrane (T_{ty}), body (T_b), skin (T_{sk}), and coat (T_{ct}) temperatures, as well as relative humidity (RH), sweating rate (SR), total (BTG_t), external (BTG_{ex}), and internal (BTG_{in}) body thermal gradients. Details are shown in the text.

Table 2

Correlation coefficients of several thermal parameters versus both of ambient temperature (T_a) and sweating rate (SR) in dromedary camels reared under natural/shaded environment.

Thermal parameters ^a	Correlation coefficients (r)			
	T_a		SR	
	Whole dataset	Average dataset	Whole dataset	Average dataset
Ambient temperature (T_a)	–	–	0.91	0.96
Relative humidity (RH)	–0.83	–0.88	–0.92	–0.97
Tympanic temperature (T_{ty})	0.39	0.57	0.54	0.67
Rectal temperature (T_r)	0.76	0.93	0.84	0.95
Skin temperature (T_{sk})	0.82	0.87	0.83	0.96
Coat temperature (T_{ct})	0.96	0.99	0.92	0.97
Body temperature (T_b)	0.82	0.96	0.92	0.95
Sweating rate (SR)	0.91	0.96	–	–
Total body thermal gradient (BTG_t)	0.97	0.99	0.91	0.96
External body thermal gradient (BTG_{ex})	0.97	0.99	0.90	0.93
Internal body thermal gradient (BTG_{in})	0.70	0.78	0.70	0.89

^a Details are shown in the text.

while T_{sk} especially in thinly insulated and shaded surfaces (“body thermal windows”; Morrison, 1966) are usually higher than T_r under thermal stressful conditions (Al-Haidary, 2006; Tattersall et al., 2009; Abdoun et al., 2012). In the present experiment, both of T_r and T_{sk} were highly correlated to T_a and SR (Table 2), but T_{sk} alone was strongly interrelated to SR (Table 3, Figs. 2 and 3). Indeed, previous reports on *Bos taurus* have demonstrated that T_{sk} , but not T_r , can act as a reliable driver of sudomotor (Whittow, 1962; Berman, 1971; Scharf et al., 2008). However, Murray (1966) found that major differences between SR of shaded and unshaded *Bos taurus* were more related to T_a than T_r and/or T_{sk} .

Consequently, it seemed rational to include T_b in the analysis. The contribution of T_b was actually embraced as a result of the findings that both of T_r and T_{sk} can control the sudomotor activity in *Homo sapiens* (Gisolfi and Wenger, 1984; Yamazaki et al., 1994). Additionally, there are multiple reasons to think that basic coordination between body thermoeffectors in other mammals is likely to be achieved through their dependence on one common variable (i.e. T_b) (Lovegrove et al., 1991; Nichelmann and Tzschentke, 1995; Spiers, 2012). But again, considering the strong interrelationship of SR with T_a , it is unlikely that sudomotor in *Camelus dromedarius* depends solely on T_b . This may propose that body thermal gradient (either BTG_t or BTG_{ex}) can be the input (or more probably the combination of inputs) that drives sudomotor in this species.

Conceptually, body thermal gradient plays an important role in determining the changes in body heat content and -as a consequence-

Table 3

Linear relationships of sweating rate (SR) versus highly-correlated (measured and estimated) thermal parameters in dromedary camels reared under natural/shaded environment.

Thermal parameters ^a	Regression linear equation	R ²
Using whole-dataset		
Ambient temperature (T_a)	$SR = -80.692 + (4.726 * T_a)$	0.84
Rectal temperature (T_r)	$SR = -4152.328 + (111.466 * T_r)$	0.70
Skin temperature (T_{sk})	$SR = -899.303 + (27.445 * T_{sk})$	0.71
Coat temperature (T_{ct})	$SR = -520.638 + (16.881 * T_{ct})$	0.82
Body temperature (T_b)	$SR = -4082.525 + (110.324 * T_b)$	0.84
Total body thermal gradient (BTG_t)	$SR = 98.292 + (4.884 * BTG_t)$	0.84
External body thermal gradient (BTG_{ex})	$SR = 89.365 + (5.278 * BTG_{ex})$	0.80
Internal body thermal gradient (BTG_{in})	$SR = 138.951 + (28.062 * BTG_{in})$	0.48
Using average-dataset		
Ambient temperature (T_a)	$SR = -80.325 + (4.720 * T_a)$	0.92
Rectal temperature (T_r)	$SR = -5497.086 + (146.829 * T_r)$	0.89
Skin temperature (T_{sk})	$SR = -1063.663 + (32.022 * T_{sk})$	0.91
Coat temperature (T_{ct})	$SR = -548.682 + (17.661 * T_{ct})$	0.93
Body temperature (T_b)	$SR = -4403.239 + (118.812 * T_b)$	0.91
Total body thermal gradient (BTG_t)	$SR = 98.491 + (4.899 * BTG_t)$	0.92
External body thermal gradient (BTG_{ex})	$SR = 89.524 + (5.251 * BTG_{ex})$	0.87
Internal body thermal gradient (BTG_{in})	$SR = 159.567 + (39.068 * BTG_{in})$	0.82

^a Details are shown in the text.

the corresponding thermoeffector homeostatic responses like perspiration. In fact, according to Webb's theory of controlling body-heat content, thermoregulatory mechanisms are constantly working under all conditions toward achieving a state of body thermal balance by controlling body-heat content and not body-temperature level (Webb, 1995, 1997; Ivanov & Webb, 2003; Ivanov, 1997, 2006). In case of a living homeotherm, as in the Gradient Calorimeter used by physicists, much of the change in body heat content occurs in the shell, where it is well known that thermally (i.e. warm and cold) sensitive skin receptors are situated at multi-layers in the skin and subcutaneous tissues, which obviously can create a transcutaneous temperature gradient. This gradient allowed a justified assumption to be made that the thermoregulatory center is capable of measuring body-heat content just by measuring the fluctuations intensity of the heat passing through the skin according to the 2nd law of thermodynamics. In fact, it has been shown in *Oryctolagus cuniculus* that thermoeffector homeostatic responses (e.g. the onsets of vasoconstriction/vasodilation) correlated precisely with this gradient (Ivanov, 2006). Moreover, both of BTG_t and BTG_{ex} were clearly observed to determine -with high R²-the changes in the rate ($W \cdot m^{-2}$) of body-heat loss, and subsequently the changes in body-heat content in *Camelus dromedarius* (Samara, 2015).

Therefore, body thermal gradient can be considered as the combination of inputs that probably drive sudomotor in camels. It is just fascinating to imagine that under thermoneutral conditions the thermoregulation center can use shell thermoreceptors (that detect temperature and not heat) to determine both the intensity (magnitude) and direction (inflow or outflow) of body heat transfer through the shell, to ultimately activate feed-back regulatory responses and defend the produced heat load through activating feed-forward anticipating responses before there is a change in the integrated mean body-temperature. Meanwhile, under thermal stressful conditions, the thermoregulatory system can aim to fight or minimize the deviations of an integrated mean body-temperature from its starting level by attaining the maximal power of the controlling active system (i.e. temperature-control systems) through its activation of various homeostatic thermoregulatory responses such as perspiration.

Factually, our results herein were more probably allude that sudomotor in *Camelus dromedarius* is regulated through BTG_t -and not BTG_{ex} - considering that T_b was estimated using the obtained reading of three temperatures (i.e. T_r , T_{ty} and T_{sk}) as well as it yielded higher R² value against SR than T_{sk} . Using this parameter, the onset of sweating (i.e. threshold) and its effective level in this species can accordingly be

determined. In fact, the obtained findings of the analysis pointed out that the onset of sweating was around a temperature range of $-17^\circ C$ [$BTG_t = -17.079 + (0.169 * SR)$, R² = 0.83, $P < 0.001$], where it started at T_a of $20^\circ C$ [$T_a = 20.051 + (0.177 * SR)$, R² = 0.84, $P < 0.001$] and T_b of $37^\circ C$ [$T_b = 37.130 + (0.008 * SR)$, R² = 0.84, $P < 0.001$]. Meanwhile, the effective level of sweating to dissipate body heat was estimated herein to be $98.29 \text{ g m}^{-2} \text{ h}^{-1}$ (Table 3). Surprisingly, Allen and Bligh (1969) reported highly consistent findings in a close camel relative (*Lama glama*), where no sweating was observed when these animals were exposed to a surrounding T_a of $20 \pm 2.5^\circ C$, while they showed a peak SR of $100 \pm 25.0 \text{ g m}^{-2} \text{ h}^{-1}$ when T_a was raised to $40^\circ C$.

5. Conclusion

Current experiment showed that eight (i.e. T_a , T_r , T_b , T_{sk} , T_{ct} , BTG_t , BTG_{ex} , and BTG_{in}) out of ten thermal parameters can be good indicators of sweating activity in *Camelus dromedarius*, but BTG_t has more possibility to be the potential driver of sudomotor, where the effect of T_a may be translated at both of the central (T_r) and peripheral (T_{sk}) thermal receptors to combine as T_b , which consequently may provide an afferent input to the hypothalamus where the resultant efferent signals are initiated to stimulate SR. Nonetheless, this interesting physiological process requires further experimentation to fully elucidate the basic functional mechanisms of *Camelidae's* thermoregulatory system involving sudomotor.

Besides, this experiment is not without limitations, where some shortcomings deserve to be noted. First of all, because our experiment mostly depended on phenotypic interrelationships, it cannot definitely confirm that BTG_t is the thermal driver of sudomotor in this species. Second, extending the experimental period to at least 72-hrs (i.e. 3 consecutive days) should be considered in future to subsequently confirm the obtained patterns herein. Third, the current method used for measuring SR (i.e. cobalt chloride) could altered the radiative properties of the animal surface, where the removing coat-hair could decreased the resistance of heat flow mainly by convection and cutaneous evaporation from skin surface to the surrounding environment and eventually modifying SR. Despite the frequent utilization of this methodology in the literature, a different methodology (Vapometer, for example) should be applied in future for measuring SR. Finally, further experiments are absolutely warranted to adequately examine the reproducibility of the obtained patterns under the effect of direct sunlight

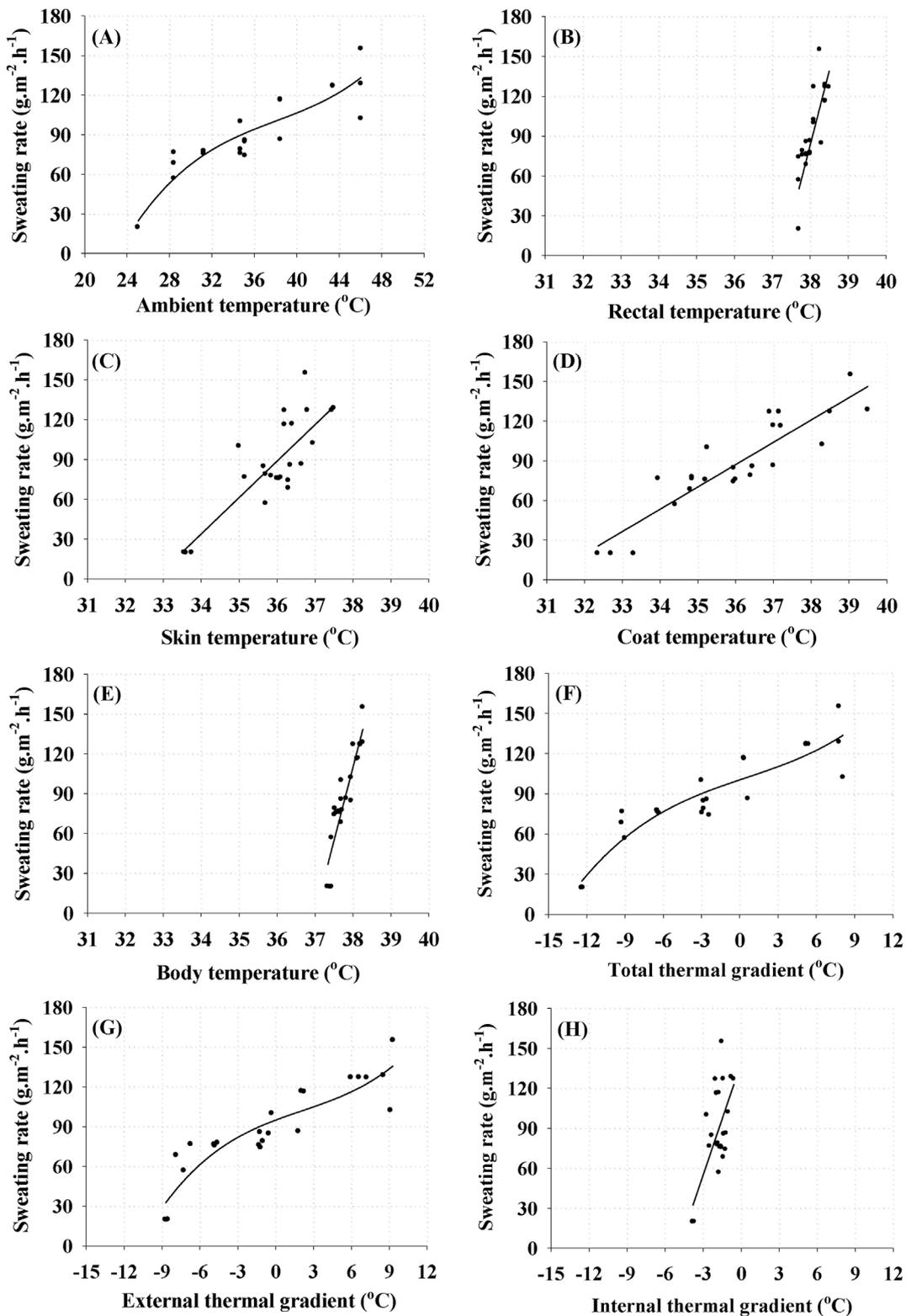


Fig. 2. Relationships of sweating rate versus highly-correlated thermal parameters (measured and estimated) in dromedary camels reared under natural/shaded environment. Refer to text for details.

as well as to study the effect of non-thermal modulators of sudomotor (e.g. exercise, dehydration and/or sympathectomy).

Compliance with ethical standards

The protocol of this experiment was carried out in accordance with

the guidelines of the Research Ethics Committee at King Saud University.

Conflicts of interest

The authors declare that no competing interests exist that are of

- to diurnal and seasonal changes. *Aust. J. Agric. Res.* 16, 92–106.
- Schmidt-Nielsen, K., Schroter, R.C., Shkolnik, A., 1981. Desaturation of exhaled air in camels. In: *Proceedings of the Royal Society of London: Biological Sciences*, pp. 305–319.
- Schroter, R.C., Robertshaw, D., Baker, M.A., Shoemaker, V.H., Holmes, R., Schmidt-Nielsen, K., 1987. Respiration in heat stressed camels. *Respir. Physiol.* 70, 97–112.
- Sejian, V., Naqvi, S.M.K., Ezeji, T., Lakritz, J., Lal, R., 2012. *Environmental Stress and Amelioration in Livestock Production*. Springer-Verlag, Berlin, Heidelberg, Germany.
- Spiers, D.E., 2012. Physiological basics of temperature regulation in domestic animals. In: Collier, R.J., Collier, J.L. (Eds.), *Environmental Physiology of Livestock*. John Wiley and Sons, pp. 17–34.
- Tattersall, G.J., Andrade, D.V., Abe, A.G., 2009. Heat exchange from the toucanbill reveals a controllable vascular thermal radiator. *Science* 325, 468–470.
- Walsberg, G.E., 1983. Coat color and solar heat gain in animals. *Bioscience* 33 (2), 88–91.
- Webb, P., 1995. The physiology of heat regulation. *Am. J. Physiol.* 268 (37), 838–850.
- Webb, P., 1997. Continuous measurement of heat loss and heat production and hypothesis of heat regulation. *Ann. N. Y. Acad. Sci.* 813, 12–20.
- Whitrow, G.C., 1962. The significance of the extremities of the ox (*Bos taurus*) in thermoregulation. *J. Agric. Sci.* 58, 109–120.
- Willmer, P., Stone, G., Johnston, J., 2000. *Environmental Physiology of Animals*. Blackwell Science Ltd., Oxford, UK.
- Yamazaki, F., Fujii, N., Sone, R., Ikegami, H., 1994. Mechanisms of potentiation in sweating induced by long-term physical training. *Eur. J. Appl. Physiol.* 69, 228–232.
- Yoshida, T., Nakai, S., Yorimoto, A., Kawabata, T., Morimoto, T., 1995. Effect of aerobic capacity on sweat rate and fluid intake during outdoor exercise in the heat. *Eur. J. Appl. Physiol.* 71, 235–239.
- Zine Filali, R., Guerouali, A., 1994. Maintenance energy requirements of the one humped camel. *J. Arid Environ.* 26, 9–13.



conferences.

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



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.



and conferences.

Aly Okab (ORCID ID: 0000-0003-2126-1122) is a professor in the Department of Environmental Studies, Institute of Graduate Studies and Research, Alexandria University. He received his PhD degree in Animal Physiology from the Department of Animal Production, Alexandria University in 1989. Then, he completed post-doctoral studies at the Slovak Agricultural research Centre (Slovakia), and held an academic position at the King Saud University (Saudi Arabia) before returning to Egypt in 2017 (Alexandria University). He has over thirty years of research experience in animal stress physiology, with an emphasis on environmental and reproduction physiology. He published more than 50 articles in international scientific research journals



Mohammed Al-Badwi (ORCID ID: 0000-0002-8282-5385) is a PhD candidate in Animal Physiology at the King Saud University. Most of his current research focuses on alleviating the adverse effects of heat stress on farm animals under sub-tropical conditions. The purpose of his work is to investigate the effects of chronophysiological management through manipulating photoperiod and feeding time under heat stress condition on goat's thermophysiology in order to ultimately enhance their performance.



external environment.

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, biollogging, biotelemetry, circadian rhythms, infrared thermography, manipulating and ameliorating the