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



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#### 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  $(T_c)$ , body  $(T_b)$ , skin  $(T_{sk})$ , coat  $(T_{c1})$  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. Ta, Tb, Tsk, Tct, BTGt, and BTGex) showed superior coefficients of determination ( $R^2 \ge 0.90$ ; 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 iregulated through BTG,. 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, was proposed according to Webb's theory of controlling body-heat content. Some shortcomings prevent confirming that BTGt 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

stitutes 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 dromedarius* is mainly a sweating species.

(Allen and Bligh, 1969; Schmidt-Nielsen et al., 1981). It was actually documented that heat dissipation through their respiratory tracts con-

Nevertheless, the mechanism of sweat stimulation (i.e. sudomotor)

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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. 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 nonadapted 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 nonthermal 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 coathair) 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 un-chopped grass hay Rhodes (*Chloris gayana* spp.) that offered twice daily (06:00 & 17:00 h) at 75 Kcal per kg<sup>0.75</sup> 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 (HOBO–U12, Onset Computer Corporation, Pocasset, USA) with a dimension of  $75 \times 60 \times 20$  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<sup>™</sup> Thermometer, Friendswood, TX, USA) with a temperature range of -22 to 110 °C, a resolution of 0.10 °C, an accuracy of  $\pm$  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  $T_{\rm r}$ ,  $T_{\rm ty}$  and  $T_{\rm sk}$ , mean body temperature ( $T_{\rm b}$ ) was estimated according to McLean et al. (1982, 1983). In fact, changes in these temperatures were related by the equation:  $[\Delta T_{\rm b} = \alpha \cdot \Delta T_{\rm r} + (1-\alpha) \cdot \Delta T_{\rm sk}]$ , where the value of  $\alpha$  was found in our case herein to be 0.87 (SE < 0.03). Additionally, the formulas;  $[T_{\rm a}-T_{\rm b}]$ ,  $[T_{\rm a}-T_{\rm sk}]$ , and  $[T_{\rm sk}-T_{\rm b}]$  were utilized to estimate the total ( $BTG_{\rm t}$ ), external ( $BTG_{\rm ex}$ ), and internal ( $BTG_{\rm in}$ ) 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  $T_{\rm sk}$  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* (g·m<sup>-2</sup>·h<sup>-1</sup>) 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 PDIFF 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 (PC1 and PC2) 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 "Wholedataset" 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.

# 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.

#### Table 1

Descriptive analysis of all measured and estimated thermal parameters.

Thermal parameters <sup>a</sup>	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 <sub>ex</sub> )	-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		

<sup>a</sup> Details are shown in the text.

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  $86.39 \text{ g m}^{-2} \text{h}^{-1}$  (SE = 7.23), the educed rhythm of *SR* in dromedary bulls was abruptly increased from a nadir value of  $19.64 \text{ g m}^{-2} \text{h}^{-1}$  at the morning (06:00 h) to a zenith value of  $154.96 \text{ g m}^{-2} \text{h}^{-1}$  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*<sub>in</sub>, 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 ( $R^2 \ge 0.80$ ; P < 0.001) linear relationships of *SR* were versus all parameter except  $T_{\rm r}$ ,  $T_{\rm sk}$ , and  $BTG_{\rm in}$ . Notably, however, only six parameters (i.e.  $T_{\rm a}$ ,  $T_{\rm ct}$ ,  $T_{\rm sk}$ ,  $T_{\rm b}$ ,  $BTG_{\rm t}$ , and  $BTG_{\rm ex}$ ) were the most relevant parameters based on the PCA, as they were strongly correlated ( $R^2 \ge 0.90$ ; P < 0.000) with the PC<sub>1</sub> (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 ( $R^2 \ge 0.90$ ; 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  $T_{sk}$ , 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



**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 <sup>a</sup>	Correlation coefficients (r)							
	T <sub>a</sub>		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 <sub>t</sub> )	0.97	0.99	0.91	0.96				
External body thermal gradient (BTG <sub>ex</sub> )	0.97	0.99	0.90	0.93				
Internal body thermal gradient ( <i>BTG</i> <sub>in</sub> )	0.70	0.78	0.70	0.89				

<sup>a</sup> Details are shown in the text.

*Bos taurus* have demonstrated that  $T_{\rm sk}$ , but not  $T_{\rm r}$ , 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  $T_{\rm a}$  than  $T_{\rm r}$ 

and/or  $T_{\rm sk}$ .

Consequently, it seemed rational to include  $T_{\rm b}$  in the analysis. The contribution of  $T_{\rm b}$  was actually embraced as a result of the findings that both of  $T_{\rm r}$  and  $T_{\rm sk}$  can control the sudomotor activity in *Homo sapiens* 

# 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 <sup>a</sup>	Regression linear equation	$\mathbb{R}^2$
Using whole-dataset		
Ambient temperature $(T_a)$	$SR = -80.692 + (4.726 * T_a)$	0.84
Rectal temperature (T <sub>r</sub> )	$SR = -4152.328 + (111.466 * T_r)$	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 $(T_b)$	$SR = -4082.525 + (110.324 * T_{\rm b})$	0.84
Total body thermal gradient (BTG <sub>t</sub> )	$SR = 98.292 + (4.884 * BTG_t)$	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 <sub>a</sub> )	$SR = -80.325 + (4.720 * T_a)$	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 $(T_b)$	$SR = -4403.239 + (118.812 * T_{\rm b})$	0.91
Total body thermal gradient (BTG <sub>t</sub> )	$SR = 98.491 + (4.899 * BTG_t)$	0.92
External body thermal gradient $(BTG_{ex})$	$SR = 89.524 + (5.251 * BTG_{ex})$	0.87
Internal body thermal gradient (BTG <sub>in</sub> )	$SR = 159.567 + (39.068 * BTG_{in})$	0.82

<sup>a</sup> Details are shown in the text.

(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 consequencethe 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 R<sup>2</sup>-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 bodytemperature. 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. temperaturecontrol 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<sub>t</sub> -and not BTG<sub>ex</sub>considering that  $T_{\rm b}$  was estimated using the obtained reading of three temperatures (i.e.  $T_r$ ,  $T_{tv}$  and  $T_{sk}$ ) as well as it yielded higher R<sup>2</sup> 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 °C  $[BTG_t = -17.079 + (0.169 * SR), R^2 = 0.83, P < 0.001]$ , where it started at  $T_a$  of 20 °C [ $T_a = 20.051 + (0.177 * SR)$ ,  $R^2 = 0.84$ , P < 0.001 and  $T_{\rm b}$  of 37 °C [ $T_{\rm b} = 37.130 + (0.008 * SR)$ ,  $R^2 = 0.84$ , P < 0.001]. Meanwhile, the effective level of sweating to dissipate body heat was estimated herein to be  $98.29 \text{ gm}^{-2} \text{h}^{-1}$  (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 °C, while they showed a peak SR of 100  $\pm 25.0 \,\mathrm{g \, m^{-2} \cdot h^{-1}}$  when  $T_{\rm a}$  was raised to 40 °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.



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.

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. 3.** A biplot verifying the dissimilarity patterns according to sweating rate (*SR*) under 2 principal components (PC<sub>1</sub> and PC<sub>2</sub>), where they both represented 95·12% of the total variance (PC<sub>1</sub> accounted for 83·41%, while PC<sub>2</sub> had 11·70%). The thermal variables utilized in this analysis are: ambient ( $T_a$ ), rectal ( $T_r$ ), body ( $T_b$ ), skin ( $T_{sk}$ ), and coat ( $T_{ct}$ ) temperatures, as well as total ( $BTG_t$ ), external ( $BTG_{ex}$ ), and internal ( $BTG_{in}$ ) body thermal gradients.

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 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.2019.102413.

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