

MODELLING ANIMAL SYSTEMS RESEARCH PAPER

The evaluation of a dynamic, mechanistic, thermal balance model for *Bos indicus* and *Bos taurus*

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SUMMARY

The Thompson model (Thompson *et al.*, *in press*), a heat balance model for cattle, was evaluated for *Bos indicus* and *B. taurus* under different climate conditions through the use of two local and one global sensitivity analyses and tested against independent datasets. The local analyses, which evaluate the individual effects of parameters on model output, showed that the vasodilation/vasoconstriction parameter and reference body temperature (T_{bref}) strongly affected body temperature. The global analysis, which evaluates the overall effect of parameters on model output, showed that 6 out of 24 parameters account for 0.79–0.89 of the model variation. The high proportion of variation accounted for by the parameters demonstrates that the model is linear in its parameters, with little interaction between the parameters.

The Thompson model was tested against four independent datasets which included both *B. indicus* and *B. taurus* animals. The prediction of the relationship between skin and body temperature from the model aligned closely with the relationship in the datasets (R^2 ranged from 0.55 to 0.87, mean bias ranged from 0.32 to 1.49). The prediction of sweating and respiration rates from the model aligned closely with the rates measured in the datasets (R^2 ranged from 0.80 to 0.98 and 0.79 to 0.93, respectively). The delay in the diurnal body temperature variation, relative to air temperature, was more accurately predicted for cattle in the sun than for cattle in climate chambers. Given the limited datasets for construction and parameterization (both of which are described in Thompson *et al.*, *in press*), the model evaluated in the current study performed relatively well compared to the literature and known biology.

INTRODUCTION

The present paper evaluates the mathematical heat balance model described in Thompson *et al.* (*in press*). The heat balance model predicts body and skin temperatures and physiological responses such as sweating and respiration rates based on the breed and body characteristics of the animal and climate factors. Since this is the first heat balance model for cattle which is both dynamic and mechanistic, it can be useful in determining heat stress in livestock as well as guiding research in heat stress. A mechanistic model should account for all the major physiological processes related to thermoregulation and for the differences between species. Therefore, livestock producers and researchers can use the model to plan research, and to

determine and then mitigate the detrimental effects of heat stress.

A thorough evaluation of a functional heat balance model requires a sensitivity analysis and a comparison against independent data. A sensitivity analysis quantifies the sensitivity of model outputs to its internal parameters. The technique is useful for ranking the importance of model parameters and their contribution to the behaviour and variation of model outputs (Saltelli *et al.* 2008). In addition, the results of the sensitivity analysis can be used as a decision-making tool to guide future experiments, by identifying which measurements would be most helpful for both estimating heat balance in the animal and evaluating the predictive ability of the model. The current study evaluates the Thompson model (*in press*) with the use of three different sensitivity analyses and by testing model predictions against independent datasets from

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Allen (1962), Brown-Brandl *et al.* (2003, 2005) and Finch (1985).

MATERIALS AND METHODS

Model description

The model equations and methods for simulation are detailed in Thompson *et al.* (*in press*). The Thompson model is a heat balance model for growing and mature cattle, and is comprised of three state variables that represent the heat content in the body-core layer, the skin layer and the coat layer (J). The body core loses heat directly through the lungs (both sensible and latent heat loss) and it exchanges heat with the skin layer (all heat exchange variables are in W ; $W=J/s$). The skin layer exchanges heat with the body-core and coat layers and it loses heat directly through cutaneous evaporation. The coat layer exchanges heat with the skin layer and with the environment, the latter being through convection, solar radiation and long-wave radiation (McArthur 1987).

In the Thompson model, as cattle experience heat stress, three physiological processes are implemented to decrease body temperature: vasodilation, and increased respiration and sweating rates. These processes increase heat loss over all state variables (body core, skin and coat).

The environmental inputs into the Thompson model are air temperature, wind speed, humidity and solar radiation. The Thompson model has parameter-specific inputs/values for *B. indicus* and *B. taurus*. The current paper evaluates the Thompson model across both species through a sensitivity analysis and a prediction evaluation against independent datasets.

Sensitivity analysis

The sensitivity analysis consisted of measuring the sensitivity of the model outputs on 24 model parameters. The sensitivity is a dimensionless variable that can be defined as the change in model outputs with respect to the change in model parameters. Theoretically, the absolute value of sensitivity ranges from zero to infinity, but for practical purposes, a value approaching 1.0 or greater is considered sensitive. Thus, a high sensitivity indicates that a specific model parameter is influential. Three forms of sensitivity analysis were conducted on the Thompson heat balance model: two local sensitivity analyses (*Local I* and *Local II*) and one global sensitivity analysis (*Global*).

Global was run under parameter changes ranging from 1 to 10%, which resulted in $\pm 3\%$ being the most realistic range of body temperature. The local analyses were then run at the same change, $\pm 3\%$, in parameter values. The local sensitivity analyses consist of an evaluation of the effect of each of the parameters on the state variables either at steady state (*Local I*) or dynamically (*Local II*). The *Local I* involves constant climate inputs while the *Local II* involves the daily fluctuations in the climate variables: temperature, wind speed, humidity and solar radiation. All sensitivity analyses use the climate input information from weather stations in Davis, CA, in the year 2006, Julian day 172 (which represents 'hot' climate conditions), where air temperature ranged from 17.7 to 37.2 °C, solar radiation reached 973 W/m², relative humidity ranged from 14 to 49% and wind speed ranged from 2.3 to 5.6 m/s. All 24 parameters in the model were run through the sensitivity analyses, and the 13 most sensitive are defined in Table 1. All sensitivity analyses were conducted with body temperature (T_b , K), calculated from body-core heat content, as the response variable because it has a much greater pool of heat in comparison to skin heat content.

Local I

In the *Local I* analysis, all input parameters and climate variables are set to predefined values; one parameter is adjusted and then the model is rerun. The resulting change in the response variable, ∂T_b , can then be used to calculate the sensitivity (S , dimensionless) of the changed parameter as follows:

$$S = \left(\frac{\partial T_b}{\partial p} \right) \times \left(\frac{\bar{p}}{\bar{T}_b} \right) \quad (1)$$

where \bar{T}_b and \bar{p} are the original (mean) values for the output and the parameter, respectively (the parameter of interest can be any one of the 24 parameters included in the model), S is the sensitivity of T_b to the parameter (p). The percent change in the parameter (∂p , %), was set to $\pm 3\%$ for *Local I* to correspond with the value determined through *Global* and after the determination that below this value the sensitivity of T_b remained linearly related to changes in the parameter. In order to run *Local I*, climate inputs were set to constant values which referred to a set point in time, e.g. the climate set at 01:30 h, and the model run until T_b reached steady state. Once steady state was reached, the value of T_b was input into Eqn (1) (as \bar{T}_b), and the model was rerun with a parameter adjusted by

Table 1. The sensitivity values of parameters evaluated with Local I and Local II for *Bos taurus* under hot conditions at 14:00 h

Parameter	Definition	Units	Local I		Local II	
			Rank	Value	Rank	Value
a_{rr}	Respiration rate parameter (intercept)	breaths/min	1	0.393	1	1.149
b_{rr}	Respiration rate parameter (slope)	breaths/(K × min)	2	0.363	2	1.075
b_{sr}	Sweating rate parameter	/°C	3	0.343	3	0.988
T_a	Air temperature	°C	4	0.176	4	0.553
b_A	Animal surface area parameter	m ² /kg ^{0.57} M_b	5	0.109	6	0.293
M_b	Body-core mass	Kg	6	0.094	17	0.080
a_{DMI}	Feed intake parameter	kg Intake/kg M_b	7	0.074	5	0.245
T_{bref}	Reference body temperature	°C	8	0.069	10	0.107
a_{sr}	Sweating rate parameter	g/m ²	9	0.056	8	0.160
<i>Solar</i>	Solar radiation	W/m ² ground surface	10	0.049	7	0.170
<i>MEC</i>	ME concentration	J/kg DM	11	0.043	9	0.145
<i>Wind</i>	Wind speed	m/s	12	0.007	20	0.020
ρ_c	Reflection coefficient of coat	Dimensionless	13	0.006	19	0.044

±3%, to calculate both ∂T_b and the sensitivity of T_b (S) for each p . This process was implemented at all of the time points from midnight to midnight in 30-min increments, calculating the change in sensitivity throughout the day. All model parameters were tested in the current analysis.

Local II

Local II is a common local sensitivity analysis in which one parameter is changed and the model then runs dynamically for 24 h (due to varying climate inputs) (Turanyi 1990). With the use of Eqn (1), the difference between the output variable calculated with the original parameter value and that calculated with the adjusted parameter value (parameter ±3%) was calculated continuously over the 24-h run time. *Local II* differs from *Local I* in that *Local II*, the change in T_b at any given time point, is a function of both the adjusted parameter value and the value of T_b from the previous time step. As in *Local I*, *Local II* was run for all model parameters.

Global

Global was conducted using the method described by Saltelli et al. (2008). Twenty four parameters were included in *Global*, and a parameter matrix (x_{ij} ; $i=1, \dots, 10000$ and $j=1, \dots, 24$) was constructed with each column representing a parameter and each row representing a draw from uniform distributions. The values for each parameter were drawn from 24 uniform

distributions, one for each parameter, with upper and lower bounds given as ±3% of the original value. Hence, 10000 simulations were performed, with the parameter inputs for each simulation being given by a row from the parameter matrix. The T_b outputs were saved from each run and stored in a model output matrix (y_{ik} ; $i=1, \dots, 10000$ and $k=1, \dots, 96$), with the rows being simulation outputs and the columns a time point from the model (0–24 h) in increments of 15 min. Ninety-five percent confidence intervals were calculated for each column of y with the use of the ‘quantile’ function in R (R Development Core Team 2010).

Standardization takes place in the form of a transformation by the ratio of the standard deviation of a parameter to its mean. The effect of the standardization is to remove the influence of units and place all parameters on an equal level. In a standardized regression setting, the total variation in the data equals 1.0 and each regression parameter squared describes a specific fraction of the model variance that is accounted for by variation in each structural parameter in the dynamic model. The R^2 , the coefficient of determination, from the standardized regression will be close to 1.0 if the model is linear in its parameters. The x and y matrices (X_{ij} and Y_{ik} , respectively) were normalized column-wise (thus, each column has a mean of zero and a variance of 1), with the use of the following equation:

$$X_{ij} = \frac{x_{ij} - \bar{x}_j}{\sigma_{x_j}} \quad \text{and} \quad Y_{ik} = \frac{y_{ik} - \bar{y}_k}{\sigma_{y_k}} \quad (2)$$

where \bar{x}_j and \bar{y}_k are the j th and k th column-wise mean values of parameter and model outputs, respectively; σ_{x_j} and σ_{y_k} are the j th and k th column-wise standard deviations of the parameter and model outputs, respectively; and X_{ij} and Y_{ik} are the normalized parameter and output values, respectively.

The k th set of model outputs ($Y_i(k)$) were regressed on the X_{ij} where the superscript k is used to indicate the k th ($k=1, \dots, 96$) regression model, which is given below and fitted using ordinary least square as follows:

$$Y_i^{(k)} = \sum_{j=1}^{24} \beta_j^{(k)} \times X_{ij} + e_i^{(k)} \quad (3)$$

$$i=1, \dots, 10\,000, \quad j=1, \dots, 24, \quad k=1, \dots, 96$$

where i is the number of model runs, j indexes the parameters and $e_i^{(k)}$ is the error term in the k th regression model. The betas, $\beta_j^{(k)}$, represent the change in model output standard deviation per one unit change in parameter standard deviation, which is estimated at the k th time point. In the standardized regression setting, the model output variance at the k th time point is given by linear relationships in the parameters and can be calculated as $\sum_{j=1}^{24} \beta_j^{(k)2}$. This is equal to R^2 and hence the quantity $1-R^2$ is the fraction of the model variance at the k th time point that is not explained by linear relationships between parameters. This fraction can be interpreted as the degree of nonlinearity in model output caused by interactions between model parameters. β_j^2 is the change in variance of the model output given one unit change in variance of the parameter. If $R^2 > 0.8$ then β_j^2 is an approximation of the first-order sensitivity indices as given by the modified Sobol method (Saltelli *et al.* 2008).

Global was run for each species under hot, mild and cold conditions (days 31, 124 and 172). The model was deemed sensitive to a parameter if the square of $\beta_j^{(k)}$ from the regression was greater than 0.04 at any given point throughout the day.

All sensitivity-related calculations were performed in *R*, whereas the Thompson Heat Balance model was run in Matlab (Matlab 2010; R Development Core Team 2010).

Prediction evaluation

Four datasets were used to evaluate the predictive abilities of the model, including Allen (1962), Brown-Brandl *et al.* (2003, 2005) and Finch (1985). The Allen (1962) and Brown-Brandl *et al.* (2003) datasets were

used because they contained sweating rates and/or respiration rates. The Brown-Brandl *et al.* (2005) dataset was used for fitting the respiration rate equations within the model, but was further implemented in testing the model because it provided solar radiation data, which allowed the testing of the solar radiation portion of the model. The Finch (1985) dataset was used because it reported values for the two state variables (body and skin heat content) and the environmental inputs.

Air temperature and humidity inputs were available for all datasets. Unless otherwise noted, wind speed was assumed to be zero in climate chambers. The radiant temperature of the surroundings was set equal to the air temperature in the climate chambers, and solar radiation was set to zero. The methods section in the Allen (1962) article states that animals were kept in chambers at a specific temperature for 30–40 min, then measurements were taken and the temperature was raised to the next level. Neither the time it took to raise the chamber temperature nor the time to make the measurements was included in the description. Therefore, to test this dataset, the air temperature input into the model was assumed to remain constant for 35 min and the time that it took to be raised to the next temperature level was assumed to be 10 min.

Another assumption made for the datasets involved the method for modelling heat production from feed intake. Most datasets measured feed intake (all except Allen 1962), but the metabolizable energy (*ME*) of the feed was not provided in any dataset. In addition, all of the experiments included *ad libitum* feeding immediately prior to the heat stress trials without measuring intake, which was measured only during the trials. A drop in heat production as a result of a drop in feed intake is a delayed effect; thus, because all the experiments were short in duration (max length of 24 h), heat production was assumed to be *ad libitum* heat production. *Ad libitum* feed intake was not measured in the experiments; therefore, heat production was calculated with intake being 0.02 kg/kg M_b and *ME* being 10.42×10^6 J/kg DM.

The statistics implemented to evaluate model prediction *v.* the experimental results, for the output variables T_b , skin temperature (T_s), respiration rate and sweating rate, are the *Mean bias* (°C), the root-mean-square error of prediction (*RMSEP*, °C) and the errors due to *Bias*, *Slope* and *Random* (dimensionless), as presented by Bibby & Toutenburg (1977). *Mean bias* demonstrates whether the model is over- or under-predicting, whereas *RMSEP* yields the amount of error

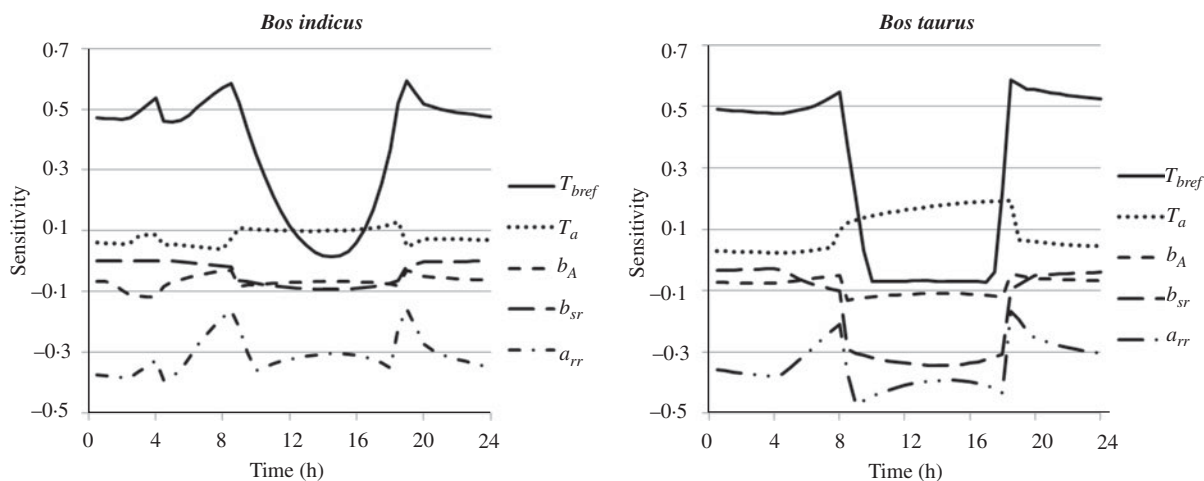


Fig. 1. Sensitivity of the most sensitive parameters on predicted body temperature (T_b) for *Bos indicus* and *Bos taurus* under hot climate conditions using *Local I*, as described in the methods. The parameters are as follows: T_{bref} is reference body temperature (a vasodilation/vasoconstriction parameter), a_{rr} is a respiration rate parameter, b_{sr} sweat is a sweating rate parameter, T_a is air temperature, and b_A is an animal surface area parameter.

of the model predictions. The statistics *Bias*, *Slope* and *Random* are the proportions of error (which sum to 1.0) due to each of those statistics.

RESULTS AND DISCUSSION

Sensitivity analysis

The most sensitive parameters are presented below and in Table 1, which includes the most sensitive parameters from *Local I* and the corresponding values for *Local II* for *B. taurus*. The sensitivity analyses were conducted for both *B. indicus* and *B. taurus* under hot, mild and cold conditions, but due to space limitations only the results for *B. taurus* under the hot conditions, which show the greatest variation in the sensitivities and model behaviour, are presented for each analysis.

Local analyses

Figure 1 shows the sensitivities of T_b for the five most sensitive parameters calculated with *Local I* for both *B. taurus* and *B. indicus* under hot climate conditions. Across all climate conditions, the T_b for *B. indicus* exhibited a greater sensitivity to T_{bref} than did the T_b for *B. taurus*. Under hot conditions, the T_b for *B. taurus* and *B. indicus* were most sensitive to respiration rate parameters (a_{rr} and b_{rr} , which are the slope and intercept for respiration rate v. body temperature, respectively, although only a_{rr} is shown in Fig. 1 as the pattern for both is similar), sweating rate parameter (b_{sr} ; g sweat/m² of skin area per hour), animal surface area

parameter (b_A), air temperature (T_a) and reference body temperature (T_{bref}) parameters. The parameters a_{rr} , b_{rr} and b_{sr} were originally predicted in Thompson *et al.* (2011). Under mild conditions for both species, body-core mass (M_b) and a feed intake parameter (a_{DMI}) were more influential than were T_a and b_{sr} . In general, as the climate cooled, most parameters decreased in sensitivity whereas T_{bref} increased in sensitivity. The parameters with the highest sensitivity are shown with their respective rankings in Table 1 for *B. taurus* and *B. indicus*.

Figure 1 shows sharp changes in the sensitivity of T_b for the all of the parameters, except T_{bref} , after sunrise and around sunset (08:00 and 18:00 h, respectively) with the inverse occurring for T_{bref} . These sudden changes result from a maximum function in the body tissue resistance (r_s , s/m) equation (Eqn (1.2) in Thompson *et al.*, *in press*). Body tissue resistance (r_s) reached a minimum, representing the maximum amount of vasodilation. Thus, a further increase in the rate of heat loss from the body resulted from increased respiration, causing a sharp increase in the sensitivity of the respiration rate parameter, a_{rr} . At high temperatures, a_{rr} is one of the most important limiting parameters of heat loss.

Changes in body heat are calculated using three variables: heat production, heat flow to the skin and heat loss through respiration (Eqns (1.10), (1.1) and (1.3), respectively in Thompson *et al.*, *in press*). Heat loss from the body is impacted by the limit in heat flow to the skin (a flow driven by r_s), increasing the impact of

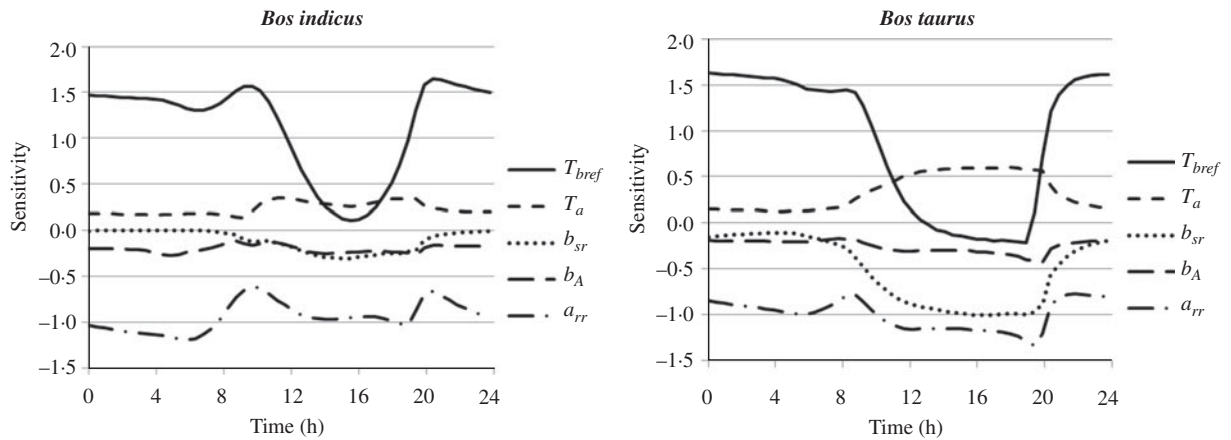


Fig. 2. Local II sensitivity analysis for *Bos indicus* and *Bos taurus* under hot climate conditions. The figures are the sensitivity of the model parameters on body temperature (T_b) where T_{bref} is the reference body temperature (a vasodilation/vasoconstriction parameter), T_a is the air temperature, b_{sr} is a sweating rate parameter, b_A is an animal surface area parameter and a_{rr} is a respiration rate parameter (intercept).

the other variables on body temperature. Respiration losses compensate for the minimum value reached in r_s ; therefore, the sensitivity of T_{bref} , a parameter which drives r_s , inversely correlates with the sensitivity of the respiration rate parameters. The sensitivity of T_{bref} does not decrease to zero as r_s reaches a minimum because it is also an input for heat production (as a basis in the maintenance requirement calculation; Eqn (1.11) in Thompson *et al.*, *in press*), although the effect of T_{bref} on heat production is small compared with that on heat flow to skin. The sharp increases in the respiration rate parameters cause the sudden changes in sensitivity seen in the other parameters (Fig. 1).

Figure 2 shows the effect of the most sensitive parameters, a_{rr} , T_{bref} , b_{sr} , b_A and T_a , on T_b for *B. taurus* and *B. indicus* under hot conditions calculated with Local II. The parameters a_{rr} and b_{rr} most strongly affected body temperature during the day for both species, but due to the great extent of the overlap, only a_{rr} is shown in Fig. 2. T_{bref} exhibits the greatest effect on T_b at night for both species. The T_b of *B. taurus* was more sensitive to the parameters b_A , T_a and b_{sr} than was that of *B. indicus* although both species had relatively low sensitivities to these parameters compared with T_{bref} and a_{rr} . The T_b of both *B. taurus* and *B. indicus* were less sensitive to all model parameters under cold conditions. The parameters b_A and M_b were more important than were respiration rate parameters for *B. indicus* under cold conditions (results under cold conditions are not shown).

Table 1 shows the top 13 most sensitive parameters analysed with Local I and the rank of those parameters

analysed with Local II. The top four ranked parameters for both analyses are identical in order, although their sensitivity values are different, where Local II in general has higher sensitivity values than Local I. Reference body temperature is not among the top ranking parameters because the time point for the table is 14:00 h, at which the model has a low sensitivity to T_{bref} (Figs 1 and 2). The ranks of the next eight parameters are not as closely aligned between Local I and Local II, but these parameters have low sensitivity and little impact on the model outputs. Thus, both analyses yield similar information about the model parameters, which demonstrates that either analysis may be sufficient.

Local II is more commonly used than is Local I for dynamic models. With Local II, the change in a response variable, such as T_b , is dependent on the change of not only a parameter, but also the value of the response variable from the previous time step, as illustrated by the reflection coefficient of the coat, ρ_c . For example, there is zero sensitivity of the model outputs to ρ_c before sunrise when both Local II and Local I are run (this example is for explanatory purposes; results not shown). At sunrise, sensitivity to ρ_c enters into the model, and theoretically it should leave at sunset, but such is not the case in Local II, as T_b does not quite return to the original value. Local I does not depend on the previous time step and the sensitivity of T_b on ρ_c does return to zero. This independence from the previous time step can be seen as strength of Local I, as it helps in the understanding of the model equations and behaviour

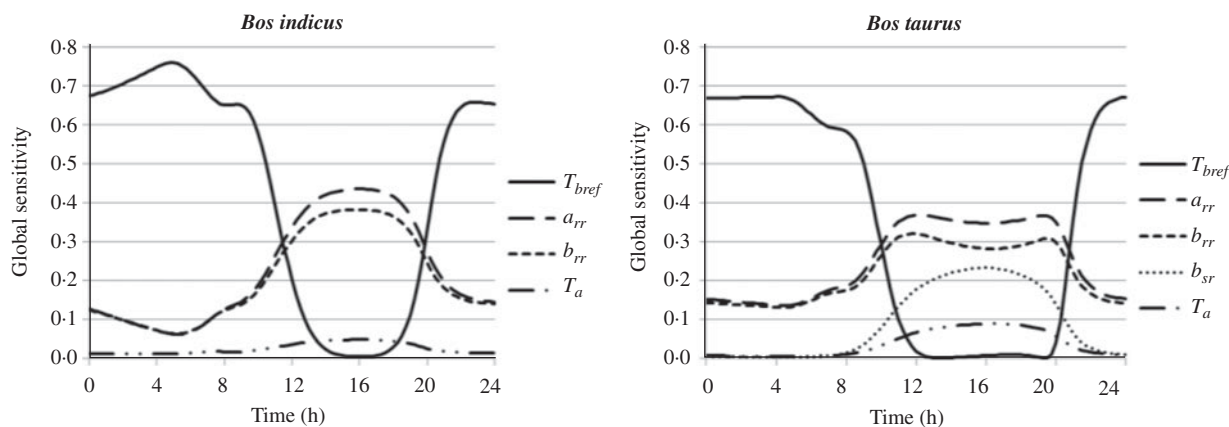


Fig. 3. Sensitivity indices for body temperature (T_b) from *Global* for *Bos indicus* and *Bos taurus* under hot conditions plotted over 24 h. The parameters included are those whose sensitivity indices are greater than 0.04 at any given time point throughout the day. Here T_{bref} is a vasodilation parameter, a_{rr} and b_{rr} are the respiration rate parameters, b_{sr} is a sweating rate parameter and T_a is air temperature. Some of these lines overlap. These sensitivities represent the proportion of total variation in the model accounted for by each parameter.

at a fixed point in time. On the other hand, *Local II* better describes the effect of a change in a parameter on the output over time by accounting for the previous time step, i.e. it smoothes model variance. Moreover, model dynamics depend on the previous time steps because the rate is a function of state, i.e. rate-state-formalism.

The T_{bref} and respiration rate parameters were found to be the most sensitive in the model with the use of either *Local II* or *Local I*. *Local I* was more sensitive to the conditional statements (if/then and max and min functions) in the model. Both analyses appear to be useful, but *Local I* may be a better means of understanding the equations and their functional relationship with the parameters, whereas *Local II* may be a better means of understanding the effect of the parameters on model behaviour. Both analyses yield similar results; thus, *Local II* may be more appropriate with less computation time for dynamic models because it is easier to implement and it will output dynamic sensitivities.

Global

The high *Global* R^2 value ranging from 90.4 to 95.4 (using the most sensitive parameters, for *B. indicus* and *B. taurus*, respectively), demonstrates that the model is linear in its parameters (Saltelli *et al.* 2008). Figure 3 presents sensitivity (β_j^2) for the selected model parameters plotted against time for both cattle species under hot conditions, where the parameters T_{bref} , a_{rr} , b_{rr} , b_{sr} , T_a and b_A were most sensitive. The R^2

quantifies the proportion of the total model variance that is explained by linear combinations of the parameters. For *B. taurus*, the most important parameters (sensitivity indices >0.04) explained 0.88–0.99 of the model variation (Fig. 3). The proportion of the variation accounted for by the parameters increased from 0.94 to 1.00 when all of the parameters were included. Therefore, most of the model variation can be accounted for by just a few parameters (T_{bref} , a_{rr} , b_{rr} , b_{sr} and T_a). The parameters T_{bref} , a_{rr} , b_{rr} and b_{sr} were the only ones contributing 10% or more to the model variation under hot conditions. Given this outcome, the future experiments can focus on measurements of only the most important parameters as long as the other parameters have been adequately described. The Thompson model is a relatively complex mechanistic model, but its use in a specific situation requires fitting of only the three to five parameters to which the model outputs are most sensitive. The estimates for the other parameters are sufficient and do not have to be estimated specifically because their sensitivity is relatively low.

Figure 4 shows T_b over time for both *B. indicus* and *B. taurus* under hot conditions. The confidence intervals are constant over time, except those for *B. indicus*. The symmetry of the confidence intervals demonstrates that the model variation is independent of time, meaning sensitivity to variation in model parameters over time remains of similar magnitude. Figure 3 helps to explain the narrowing of the confidence intervals during the day for *B. indicus* under hot conditions. For *B. indicus*, only the two

Table 2. Model inputs used from evaluation datasets

Variable/parameter	(Allen 1962)	(Finch 1985)	(Brown-Brandl <i>et al.</i> 2003)	(Brown-Brandl <i>et al.</i> 2005)
Air temperature (°C)	18–41	25–46	11–41	15–35
Solar radiation max (W/m ²)	0	0	0	0–881
Relative humidity (%)	45–55	37–50	21–76	41–97
Wind speed (m/s)	0.6	0	0	1.1–4.9
Body weight (kg) <i>B. taurus</i>	320	380	330	378
Body weight (kg) <i>B. indicus</i>	320	395	N/A	N/A

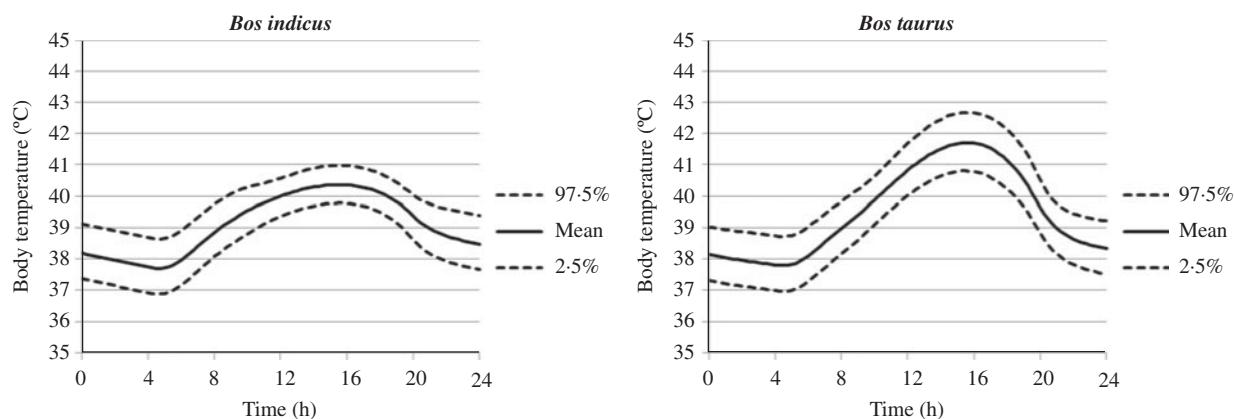


Fig. 4. Predicted mean body temperature (solid line) and upper (97.5%) and lower (2.5%) confidence intervals (dashed lines) for *Bos indicus* and *Bos taurus* under hot conditions. The uncertainty around the predicted mean body temperature is due to $\pm 3\%$ uncertainty implemented in the structural parameters of the heat balance model as described in the methods.

respiration rate parameters greatly increase in sensitivity during the day, while that of T_{bref} is small. For *B. taurus*, the sensitivity of four parameters increases during the day followed by a concomitant decrease in the sensitivity of T_{bref} , thus, the confidence interval for them does not decrease.

The variation in the model that is not accounted for by a linear relationship with parameters (0.001–0.062) is accounted for by non-linear relationships, which are the interactions between the parameters (Saltelli *et al.* 2008). A great deal of computing time (> 375 h, using 20+ parameters in Matlab) is required for calculating these interactions. As the relative contribution of the interaction to model variance was small, these calculations were not performed. The information about model variance and the contribution of the different parameters given by *Global* cannot be obtained through a local sensitivity analysis, thus making *Global* a vital addition to model evaluation (Figs 3 and 4). In addition, *Global* can be used as a guide to data collection in experiments and as a means for further development of mathematical models.

Prediction evaluation

The species and climate inputs used to evaluate the model against the datasets are shown in Table 2. Figure 5 shows the reported values for skin *v.* body temperatures and sweating rates *v.* skin temperature from the Allen (1962) dataset and the predicted values from the model for *B. indicus* and *B. taurus* cattle, respectively, the statistical calculations for which can be seen in Tables 3 and 4. The statistical calculations are the results of the predicted and experimental data for both skin *v.* body temperature and for skin *v.* air temperature. The skin *v.* body temperature plots show that the model accurately predicts this relationship for both species, although the model does not contain stochastic variables and, therefore, does not account for random variation. Sweating rates for *B. indicus* are predicted with a low *Bias* and *Slope*; however, the rates have a low *Bias* for *B. taurus*, but a large *Slope*.

The comparison of the model predicted body temperature with reported body temperature, for the given air temperature (Table 4), shows that *Bias* and

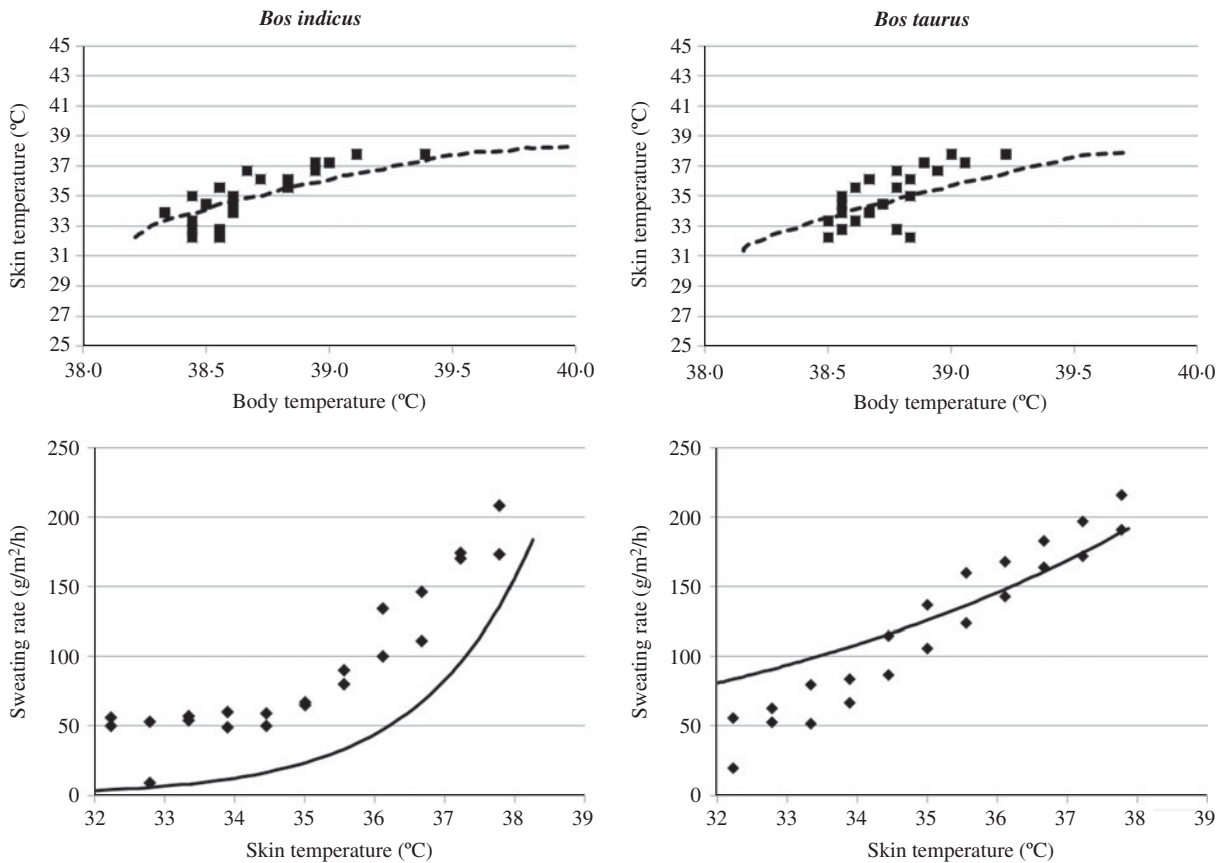


Fig. 5. Model predictions of the relationship between skin and body temperature ($^{\circ}\text{C}$) and between sweating rate ($\text{g}/\text{m}^2/\text{h}$) and skin temperature compared with the Allen (1962) dataset for *Bos indicus* and *Bos taurus*. All lines are simulated data (solid lines are sweating rate and dashed lines are skin temperature), whereas the points are experimental data (squares are skin temperature and diamonds are sweating rate).

Slope combined for both species are responsible for the majority of the error, perhaps because of the timing of the rise in room temperature. The Allen (1962) article does not provide the time it took for the room temperature to increase or the time it took for measurements to be taken. Therefore, estimates of the timing of those events were made, which impact both the slope and the shape of the simulated body temperature curve (Table 4).

The R^2 for the sweating and respiration rate predictions (0.80–0.98 and 0.79–0.93, respectively) of the Allen (1962) dataset for both species are higher than those for the T_b and T_s predictions (0.51–0.84) (results not shown). *Random* is responsible for the majority of the error (0.36–0.76) for the T_s v. T_b predictions for all the treatments except for one Jersey treatment. A large *Random* indicates that the model's predictions do not exhibit a large *Bias* or *Slope*, and thus the fit cannot be further improved with the given model (Table 3).

The Thompson model (Thompson *et al.*, *in press*) predictions for body and skin temperatures v. air temperatures and skin v. body temperatures for the Finch (1985) dataset are shown in Fig. 6, the statistical calculations for which are in Tables 3 and 4. The model predictions for *B. taurus* (Shorthorn) body and skin temperatures more closely aligned with the Finch dataset than did the predictions for *B. indicus* (Brahman) body and skin temperatures, although temperatures were overpredicted for both species. The model under-predicted skin temperature compared with body temperature as body temperature neared 39°C , but otherwise predicted the skin v. body temperature relationship accurately for both species (lower two graphs in Fig. 6). The R^2 for body v. air temperature and skin v. body temperature for both species ranged from 0.79 to 0.96, with *Bias* contributing the majority of error (0.61–0.96) (Tables 3 and 4). More information from the experiments, such as sweating and respiration rates would allow for a better

Table 3. Results of statistical analysis of model predicted skin and body temperature compared with experimental data of skin and body temperature (°C)

Reference	Breed	Mean bias* °C	R ²	Bias† %	Slope %	Random %	RMSEP‡ °C
(Finch 1985)	Brahman	1.49	0.87	86.1	8.8	5.1	1.59
	Shorthorn	0.99	0.79	61.3	8.4	30.3	1.23
(Allen 1962)	Zebu	0.32	0.55	22.0	28.4	49.6	1.75
	Jersey	0.90	0.56	25.1	26.2	48.7	1.94

* Mean bias is observed minus predicted.

† Bias, slope and random are percentage of mean-square error of prediction.

‡ Root-mean-square error of prediction.

Table 4. Results of statistical analysis of model predicted body temperature (°C) compared with experimental data, given air temperature (°C)

Reference	Treatment/species	Mean bias* °C	R ²	Bias† %	Slope %	Random %	RMSEP‡ °C
Brown-Brandl <i>et al.</i> (2003)	Mild	0.28	0.22	48.6	39.5	11.9	0.40
	Hot	0.59	0.41	69.0	6.0	25.0	0.71
Brown-Brandl <i>et al.</i> (2005)	Mild – shade	–0.07	0.46	6.2	45.0	48.7	0.29
	Mild – sun	–0.43	0.05	24.4	72.8	2.7	0.87
	Hot – shade	–0.57	0.46	70.8	19.8	9.4	0.67
	Hot – sun	–1.46	0.83	65.2	33.6	1.2	1.81
Finch (1985)	<i>B. indicus</i>	–0.94	0.96	97.1	2.5	0.4	0.95
	<i>B. Taurus</i>	–0.62	0.96	77.2	21.8	1.0	0.69
Allen (1962)	<i>B. indicus</i>	–0.41	0.57	56.6	40.7	2.8	0.53
	<i>B. Taurus</i>	–0.04	0.78	9.1	86.8	4.2	0.29

* Mean bias is observed minus predicted.

† Bias, slope and random are percentage of mean-square error of prediction.

‡ Root-mean-square error of prediction.

understanding of the *Bias* component. The over-prediction in the *B. indicus* data can be attributed to the overestimation of heat production. Heat production is difficult to estimate accurately due to the lack of feed intake information, such as the *ME* of the feed and intake levels immediately prior to the experiment.

The Brown-Brandl *et al.* (2003) dataset and predictions are shown in Fig. 7, and the statistical calculations are presented in Table 4. The model under-predicted T_b at an increasing rate as air temperature increased from a treatment average of 18–34 °C. The maximum underprediction of body temperature occurred in the time range of 20.00–22.00 h (underprediction of 1.1 °C in the 34 °C treatment). The Brown-Brandl *et al.* (2003) dataset showed that the maximum body temperature occurred 4 h after the maximum air temperature was reached, whereas the model found that the maximum body temperature occurred 1.25–2 h after the maximum air temperature was reached.

The underestimation of body temperature in the Brown-Brandl *et al.* (2003) dataset can be attributed to evaporative losses (Fig. 7). The model overpredicted evaporative losses by 189 kJ/kg^{0.75} in the 34 °C treatment and by 210 kJ/kg^{0.75} in the 30 °C treatment. The predicted evaporative loss estimates were 48 and 65% above the observed values for the 34 and 30 °C treatments, respectively. Evaporative losses accounted for 0.78–0.95 of total heat losses for the 34 and 30 °C treatment groups; thus, a large error in this estimate led to a large error in body temperature. Kibler & Yeck (1959) found evaporative heat losses to reach 458 kJ/kg^{0.75} under similarly heat stressed conditions for shorthorn beef cattle, which was above that measured by Brown-Brandl *et al.* (2003) (390 kJ/kg^{0.75}) but below the predicted evaporative heat loss of 579 kJ/kg^{0.75}. The large overestimation of evaporative heat loss alone would cause a greater disparity between measured and simulated body temperatures. However, the large predicted evaporative losses

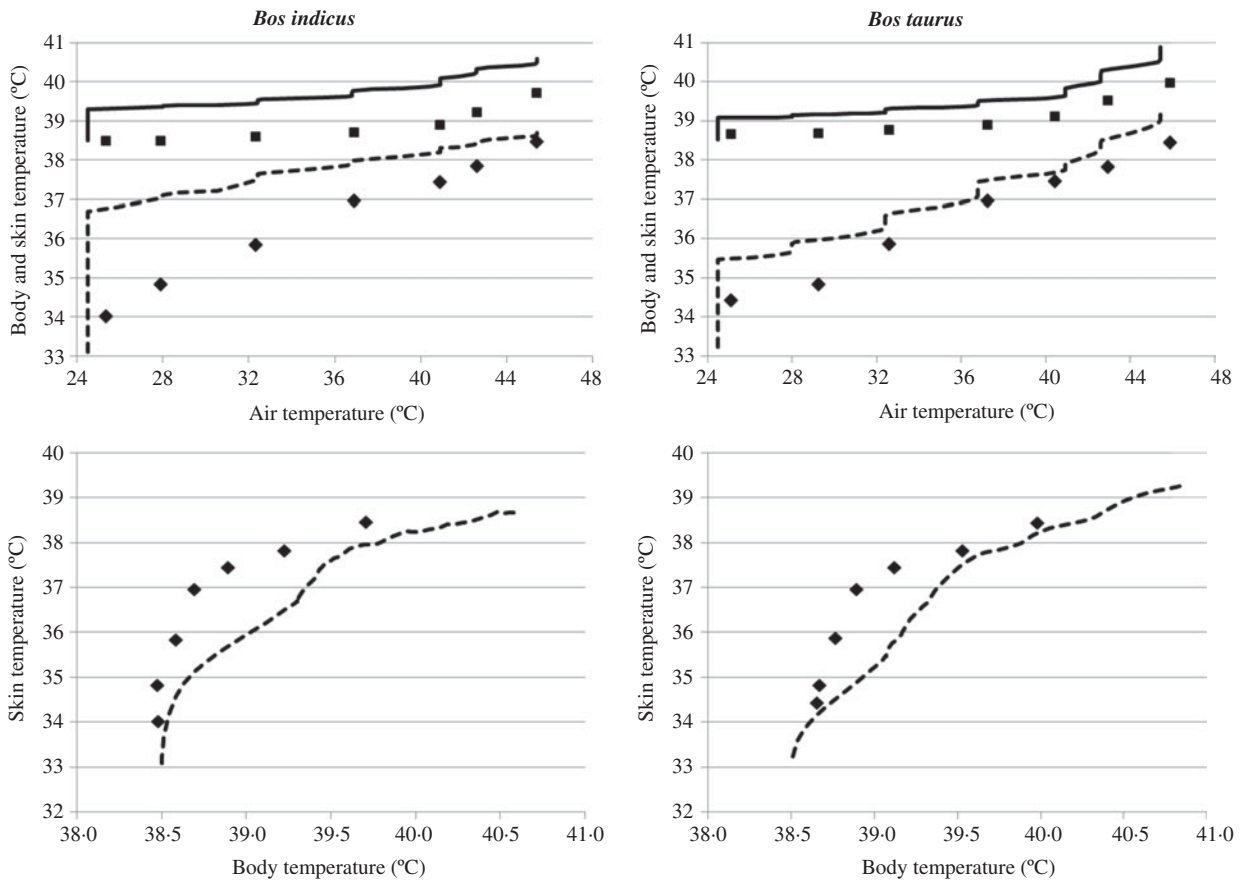


Fig. 6. Model predictions of the relationships among body temperature, skin temperature and air temperature (°C) compared with the Finch (1985) dataset for *Bos indicus* and *Bos taurus*. All lines are simulated data (solid lines are body temperature and dashed lines are skin temperature), whereas the points are experimental data (squares are body temperature and diamonds are skin temperature).

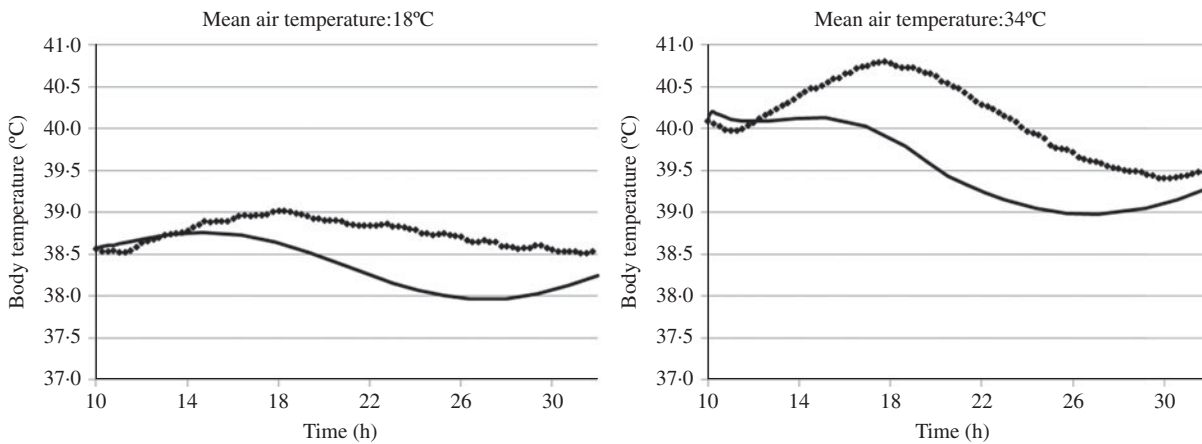


Fig. 7. Model predictions of body temperature (°C) compared with the Brown-Brandl *et al.* (2003) dataset for *Bos taurus* cattle. All lines are simulated data, whereas the points are experimental data. The mean air temperatures are 18 and 34 °C, whereas the daily fluctuations are ± 7 °C from the mean.

compensated for the higher predicted heat production compared to the observed heat production (725 v. 540 kJ/kg^{0.75}, respectively). The lower value for

measured heat production can be attributed to decreased feed intake. When the model predicted the data based on the lower intake, heat production

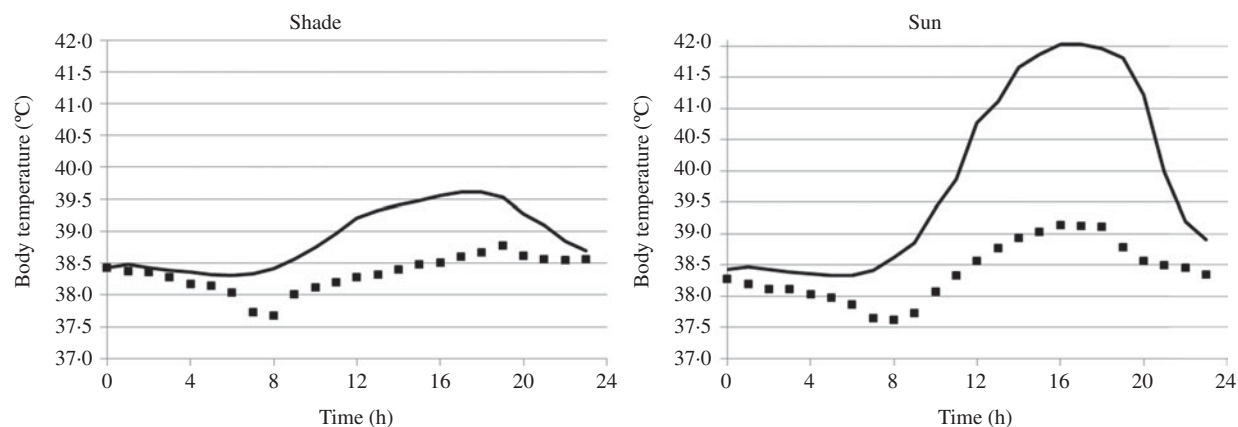


Fig. 8. Model predictions of body temperature ($^{\circ}\text{C}$) compared with the Brown-Brandl *et al.* (2005) dataset for *Bos taurus* cattle in the shade and sun. All lines are simulated data, whereas the points are experimental data.

was greatly underestimated. In the experiments, the decrease in heat production was gradual as the animals shifted from eating *ad libitum* to a reduced feed intake; thus, the measured heat production was a function of both the decreased and the *ad libitum* intake, with the actual heat production falling between the decreased and the *ad libitum* intake at steady state. The experiments did not include a delay in measuring heat production after the animals were subjected to heat stress and began to decrease intake. Therefore, heat production was calculated based on *ad libitum* feed intake.

The model does not account for heat increment of feeding and, instead, assumes constant heat production throughout the day. Sprinkle *et al.* (2000) has shown that the heat increment of feeding is dependent on the species as well as the feed energy due to differing rates of passage of feed. The assumption of constant heat production contributes to the differences in the predictions of the Brown-Brandl *et al.* (2003) dataset, in which the model consistently underpredicted body temperature. The cattle decreased their feed intake as body temperature rose, whereas the predictions were made under the assumption of a constant feed intake. Decrease in heat production lags after decrease in feed intake, but models that demonstrate this lag are scarce; thus, a constant value for intake is used (McGovern & Bruce 2000; Turnpenney *et al.* 2000). In addition, the cattle ate less as body temperature rose, yet only an average daily intake is given in the Brown-Brandl *et al.* (2003) dataset; thus, even if heat increment were implemented in the model, the decline in intake would still have to be estimated, which would have contributed to the error component.

The Thompson model (Thompson *et al.*, *in press*) demonstrated a prediction trend with the Brown-Brandl *et al.* (2005) dataset similar to that with the Allen (1962) dataset, in which the accuracy of the model decreased as heat stress increased. The model overpredicted T_b as T_a increased, with a greater overprediction for cattle under solar radiation (Fig. 8). The statistics for the Brown-Brandl *et al.* (2005) predictions are shown in Table 4. The maximum overprediction for the solar radiation treatments occurred during daylight hours, whereas the model more accurately predicted body temperature during the night. Determining the reason for overprediction under solar radiation requires more information to compare the calculation of exchange of thermal radiation with the actual exchange experienced by the animals. Few experiments have measured or calculated solar radiation absorption, leading to the use of theoretical relationships in the model in the place of empirical relationships, which may not correctly represent the system.

Some of the differences between the experimental results and model predictions across all datasets can be attributed to the delay in T_b increase compared with the rise in T_a . Predicted T_b declined more at low T_a than was demonstrated by the Allen (1962) dataset and, likewise, increased more rapidly than the dataset at high T_a , meaning that the predicted T_b was more sensitive to T_a than was the T_b for cattle in the experiment (results not shown). The predicted peak body temperature occurred at the same time as the observed data (Brown-Brandl *et al.* 2005) in Fig. 8, whereas in Fig. 7 the predicted peak body temperature occurred 2–3 h prior to the observed data (Brown-Brandl *et al.* 2003). The delay in the body temperature

rise in the observed data is a delayed response to rising T_a . Finch (1986) found a similar delay in both sweating and respiration rate as T_a increased, leading to a delayed rise in T_b . The sun treatments of the Brown-Brandl *et al.* (2005) dataset exhibited the same pattern as did the predictions, which can be attributed to the solar radiation overpowering the effect of T_a . Both the rise in solar radiation and T_b have equivalent delays in relation to the rise in T_a . The data show that the maximum solar radiation and the maximum T_b occur at the same time whereas the maximum T_a occurs later in the day.

CONCLUSION

The sensitivity analyses showed that Thompson model is primarily linear in its parameters (although highly nonlinear in time), which results in a few interactions between parameters. In addition, only the respiration rate parameters, reference body temperature, sweating rate parameters, air temperature and the surface area of animals were important in the model, given the circumstances tested. The remaining parameters can be reasonably estimated, but do not require the attention or precision that must be given to the important parameters. Both *B. indicus* and *B. taurus* had similar patterns in the sensitivity analyses, although *B. indicus* were less sensitive due to their greater tolerance for heat stress.

Some problems exist in the prediction of body temperature and improvement requires a more complete dataset, which will provide a better understanding of the contribution of the thermal flows both within the animal and between the animal and its environment. A helpful experiment to estimate the sensitive parameters and test the main heat flows in the model would be one in which skin and body temperatures are measured, in addition to sweating and respiration rates, respiratory evaporation losses and long wave radiation fluxes. An updated experiment on heat flow from the body to the skin (vasodilation) would allow for estimation of reference body temperature. This experiment should include both *B. indicus* and *B. taurus* under a wide range of temperature conditions, from heat to cold stress. Finally, an experiment should measure the effect of solar radiation, measuring the radiation intercepted and absorbed by the animal and measuring its effect on both skin and body temperature. The experiments would also need animal inputs, such as species, M_b , intake and ME content of the feed.

The heat balance model is an adaptable, mechanistic model which can evaluate and help explain the specific physiological effects of heat stress on the animal. This model can be a useful tool for designing experiments, improving animal welfare, mitigating the detrimental effects of heat stress and improving animal performance.

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