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A body temperature model for lizards as estimated from the thermal environment

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ABSTRACT

A physically based model was built to predict the transient body temperature of lizards in a thermally heterogeneous environment. Six heat transfer terms were taken into account in this model: solar radiation, convective heat flow, longwave radiation, conductive heat flow, metabolic heat gain and respiratory energy loss. In order to enhance the model predictive power, a Monte Carlo simulation was employed to calibrate the bio-physical parameters of the target animal. Animal experiments were conducted to evaluate the calibrated body temperature model in a terrarium under a controlled thermal environment. To avoid disturbances of the animal, thermal infrared imagers were used to measure the land surface temperature and the body temperature. The results showed that the prediction accuracy of lizard's transient temperature was substantially increased by the use of Monte Carlo techniques (RMSE=0.59 °C) compared to standard model parameterization (RMSE=1.35 °C). Because the model calibration technique presented here is based on physical principles, it should be also useful in more complex, field situations.

1. Introduction

The climate change debate (Parmesan and Yohe, 2003) has generated widespread interest in the response of organisms to the thermal environment (Sinclair et al., 2003). The thermal environment is especially important for ectotherms in order to control their internal body temperature and physiological functions (Row and Blouin-Demers, 2006; Sabo, 2003). Thermal conditions influence ectotherms on: (1) growth, development and survival of embryos (Angilletta et al., 2009); (2) metabolic processes such as digestion (Harwood, 1979); (3) behavioral processes such as activity (Nicholson et al., 2005; Rouag et al., 2006; Sears, 2005; Stephen and Porter, 1993), locomotion (Waldschmidt and Tracy, 1983b), microhabitat selection (Angilletta et al., 2009; Porter and James, 1979; Schofield et al., 2009); and (4) spatial distribution and life history traits of populations (Kearney and Porter, 2004; Medina et al., 2009; Porter and Tracy, 1983).

Ectotherms are organisms that control their body temperature through external means (Avila, 1995). An ectotherm controls its temperature by adjusting its behavior like re-positioning its body within a thermal environment (Bartholomew, 1966; Hammel et al., 1967). By responding to changes in the thermal landscape, the animals maintain a thermodynamic balance over an extended period of time (Barlett and Gates, 1967). For example, lizards regulate their body temperature by many activities such as climbing to the top of the bushes to bask or orienting to the direction of the sun in order to receive more radiative energy (Bennett, 2004); flattening their body on hot rocks to conduct more heat to the body (Sabo, 2003); making postural adjustments to control the area of body surface exposed to the sun or to the cool winds (Bartholomew, 1966); keeping their mouth wide open (gaping) to cool down when the body temperature might become too high (Raymond and Montgomery, 1976; Spellerberg, 1972), as well as retiring to cool locations underground or in the shade (Barlett and Gates, 1967). To quantify these thermal transfer processes, heat transfer models have been used to calculate the energy exchange between an ectotherm and the environment (Beckman et al., 1973; Blouin-Demers and Nadeau, 2005; Porter et al., 1973; Tracy, 1976, 1982).

Many researchers have set up different models with various complexities to quantify environment–animal energy exchange based on the physics of heat transfer and the known physiological properties of animals (Beckman et al., 1973; O'Connor, 1999; O'Connor and Spotila, 1992; Porter, 1967; Porter et al., 1973; Tracy,

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1976, 1982; Waldschmidt and Tracy, 1983a). For animals in general, a thermodynamic equilibrium model was developed (Porter and Gates, 1969), by considering the thermal consequence of metabolic rate, absorbed radiation, convection, conduction, long wave radiation, water loss and work done. Using desert lizards as a target species, simplified energy balance models were proposed: Porter et al. (1973) considered solar radiation, long wave radiation and convection as key independent variables, while using a two-layer concentric cylinder model to simulate the thermal properties of the target species. Later, a similar model (Waldschmidt and Tracy, 1983b) considered the effects of solar radiation, outgoing longwave radiation, convection and conduction for the body temperature of a one-noded (unibody) lizard. Some biophysical models that describe transient temperature incorporated the thermal environment, thermal capacity and physiological control of heat exchange to provide context to the incremental body temperature attained by the animals (Beckman et al., 1973; Christian et al., 2006; Schofield et al., 2009). As the nature of ectotherms' behavioral thermoregulation, when moving in a complex thermal environment, the current body temperature of an ectothermic animal depends not only on the instantaneous thermal environment, but also on the body temperatures that the animal had in the recent past and its thermal capacity (Tracy, 1982). Therefore in this study, a model was developed that takes into account the transient temperatures of lizards moving in a thermally heterogeneous environment.

As Levins (1968) pointed out, a predictive model may have generality or accuracy, but not both. On the one hand, inductive empirical models tend to be simple and ignore some complexities of the specific animals in specific environments (O'Connor and Spotila, 1992). Inductive empirical models are easy to construct and need fewer parameters, but may have a lower accuracy. They work best when used with individuals of smaller body size or simple body shape. Conversely, more complex, deductive models that aim for higher accuracy usually need more information for calibration (O'Connor and Spotila, 1992; Skidmore, 2002). But such information may be missing from the literature or difficult to estimate through measurement. For example, one can neither measure the skin depth of target animals without capturing them in the field, nor measure the conductivity coefficient outside the laboratory. Alternatively, retrieving parameters through observable data may be a method to obtain the parameters of a bio-physical model (Christian and Roger, 2001; Marsili-Libelli et al., 2003). The hard-to-measure parameters can be estimated by several search algorithms such as trying possible parameter-combinations using a look-up table to obtain a final model that delivers outputs, which fit the observed data best. These algorithms have been used to parameterize ecological models such as predator–prey models (Cao et al., 2008), algal growth models (Marsili-Libelli et al., 2003) and animal population models (Conroy et al., 1995), though not for parameter estimation of body temperature.

The objective of this study was to fine-tune a bio-physical model to predict transient temperatures of lizards. More specifically, our study aimed to predict accurately the body temperature dynamics of a lizard in any given thermal environment with a physically based model through a rigorous calibration procedure based on Monte Carlo simulation techniques. The results of the temperature prediction were validated and evaluated by an independent dataset of animal observation conducted in a controlled environment.

2. Model description

2.1. Heat exchange terms

From a physical perspective, the energy exchange between a lizard and its environment has been described by Porter's models (Porter and Gates, 1969; Porter et al., 1973). According to his models, the body temperature depends on the balance of the general energy flow, which is the sum of the solar radiation absorbed by the lizard ($Q_{solar,rad}$), the convective heat flow (Q_{conv}) and the infrared radiation (long wave radiative heat) ($Q_{longwave}$). In addition, conductive heat flow (Q_{cond}) between a lizard and the land surface, energy gain (Q_{meta}) by food intake (metabolism) and energy loss through respiration and water evaporation ($Q_{waterloss}$) were also included in his subsequent studies (Porter, 1989) as they were found to have noticeable influence on the body temperature of the animal (Clark et al., 2006; Porter, 1989; Templeton, 1970; Tracy et al., 2010). In summary, the total energy intake of a lizard in a fixed time interval (ΔQ_e) may be written as

$$\Delta Q_e = \Delta Q_{solar,rad} + \Delta Q_{conv} + \Delta Q_{longwave} + \Delta Q_{cond} + \Delta Q_{meta} - \Delta Q_{waterloss} \tag{1}$$

2.1.1. Solar radiation

The direct solar energy incident on the lizard provides heat, which is especially important for the animal when the ambient temperature is low (Porter, 1967). The incremental energy received from solar radiation $\Delta Q_{solar,rad}$ may be written as

$$\Delta Q_{solar,rad} = \alpha_L A_p Q_{solar} \tag{2}$$

whereα_L is the absorbance of lizard skin, representing the fraction of the radiative energy absorbed by the lizard. Q_{solar} is the radiation intensity in units of Wm^{-2}, and A_p is the projected lizard area for direct and scattered solar radiation. We assumed this projected area equals the vertical projected area, which is about 0.4 times of the total surface area (m^2) of the lizard A_L (Porter et al., 1973). The surface area can be estimated from the body mass of the lizard in unit of kilogram (M_{lizard}), as described in the formula deduced from (O'Connor, 1999), with empirical coefficient $a = 0.0314$:

$$A_L = a\pi (M_{lizard})^{2/3} \tag{3}$$

2.1.2. Convection

The convective heat transfer is one of the major modes of heat transfer between the environment and the lizard. The incremental energy from convection between the air and lizard's body (ΔQ_{conv}) can be expressed as

$$\Delta Q_{conv} = h_L A_{air}(T_{air} - T_{skin}) \tag{4}$$

where h_L stands for the convective heat transfer coefficient of lizard, in units of $\mathrm{W\,m^{-2}\,K^{-1}}$. We assume an arbitrary value of convective heat transfer coefficient for a wind speed less than 0.5 m/s environment as follows: $h_L = 10.45\ \mathrm{W\,m^2\,K^{-1}}$ (Porter et al., 1973). A_{air} is the skin area that is exposed in the air, which is assumed that $A_{air} = 0.9A_L$. $T_{air} - T_{skin}$ is the difference between the surrounding air temperature T_{air} and lizard skin temperature T_{skin}.

2.1.3. Net longwave radiation

The net longwave radiation ($Q_{longwave}$) is the sum of the net infrared radiation exchange to the lizard from surrounding objects. It can be derived from the Stefan–Boltzmann law:

$$\Delta Q_{longwave} = \varepsilon_{lizard} A_{down} \sigma (T_{earth}^4 - T_{skin}^4) + \varepsilon_{lizard} A_{up} \sigma (T_{glass}^4 - T_{skin}^4) \tag{5}$$

where the lizards' infrared energy income is separated into two parts: radiation from the underlying surface with a temperature of T_{earth}, as well as from the surrounding glass walls and cover of the terrarium with a temperature of T_{glass}. T_{glass} is assumed to be the same as the air temperature T_{air}. The emissivity of lizard's skin (ε_{lizard}), was set to 0.95 according to (Campbell and Norman, 1977;

Turner and Tracy, 1986). As a fraction of the total lizard area A_L, A_{down} and A_{up} are the areas of skin "facing toward" (but not contacting with) the ground surface and the sky, respectively. In this study, $A_{down}=0.3A_L$ (when standing upright) or $A_{down}=0$ (when lies down), and $A_{up}=0.6A_L$ were considered appropriate estimations (Barlett and Gates, 1967). σ is the Stefan–Boltzmann constant, which is 5.67×10^{-8} (W m^{-2} K^{-4}).

2.1.4. Conduction

Thermal conduction may be substantial for lizard's thermoregulation (Bujes and Verrastro, 2006). Following Fourier's law the heat conducted from the underlaying surface to the body Q_{cond} can be represented as

$$\Delta Q_{cond}=\frac{A_{contact}K_{lizard}(T_{earth}-T_{skin})}{\delta/2} \tag{6}$$

where $A_{contact}$ is the area lizard contacts with the ground. It depends on the posture of lizard: $A_{contact}$ was set to $0.1A_L$ when standing and $A_{contact}=0.4A_L$ when lying. K_{lizard} is the thermal conductivity and was set to 0.50 W K^{-1} m^{-1} according to Porter et al. (1973). δ is the measured average diameter of the lizard body.

2.1.5. Metabolism

Although the daily metabolism level of lizards is not as high as that of birds or mammals of equal size, a noticeable contribution of metabolism to lizards' body temperature has been observed (Bennett and Nagy, 1977; Dawson and Bartholomew, 1958). The effect of metabolism on body temperature was considered in some studies for lizards, as an increase of metabolic rate may lead to a small but significant increase of body temperature (Brown and Au, 2009). If we assume 20.9 J of heat is produced for each cubic centimeter of oxygen consumed (Porter et al., 1973), the metabolic rate (ΔQ_{meta}) can be expressed as a function of body mass (M_{lizard}) and body temperature in degrees Celsius (T_{lizard_inC}) (Clark et al., 2006):

$$\Delta Q_{meta}=0.348exp(0.022T_{lizard\_inC}-0.132)M_{lizard} \tag{7}$$

where M_{lizard} is the mass of the lizard in kilograms. T_{lizard_inC} is the core lizard body temperature in Celsius, which is assumed to be the same as the lizard's skin temperature. Because the ratio of internal to external resistance (Biot number) is very small for a lizard in a typical environment (Porter et al., 1973), the skin temperature yields a good approximation of the core body temperature (Barlett and Gates, 1967; Waldschmidt and Tracy, 1983b). This equation shows that the rate of metabolic heat increases proportionally to the body temperature.

2.1.6. Respiratory loss

The lizard's body temperature also has an impact on its respiratory water loss, which removes the latent heat of body water during vaporization. At low air temperature, energy is lost through respiration at a constant rate that is independent of the body temperature. As the temperature rises, the speed of respiratory loss increases (Templeton, 1970). It has been suggested that the energy loss corresponding to water loss for desert iguanas (*Dipsosaurus dorsalis)* could be written as

$$\begin{aligned} &\Delta Q_{resp}=0.272m_{lizard} && (T_{lizard\_inC}<20\,^{\circ}\mathrm{C})\\ &\Delta Q_{resp}=0.0836m_{lizard}e^{0.0586T_{lizard\_inC}} && (20\,^{\circ}\mathrm{C}\le T_{lizard\_inC}<36\,^{\circ}\mathrm{C})\\ &\Delta Q_{resp}=0.003m_{lizard}e^{0.1516T_{lizard\_inC}} && (T_{lizard\_inC}\ge 36\,^{\circ}\mathrm{C}) \end{aligned} \tag{8}$$

As hardly any useful data are available on the energy loss by water vaporization for *Timon lepidus* (Ocellated lizard), this study

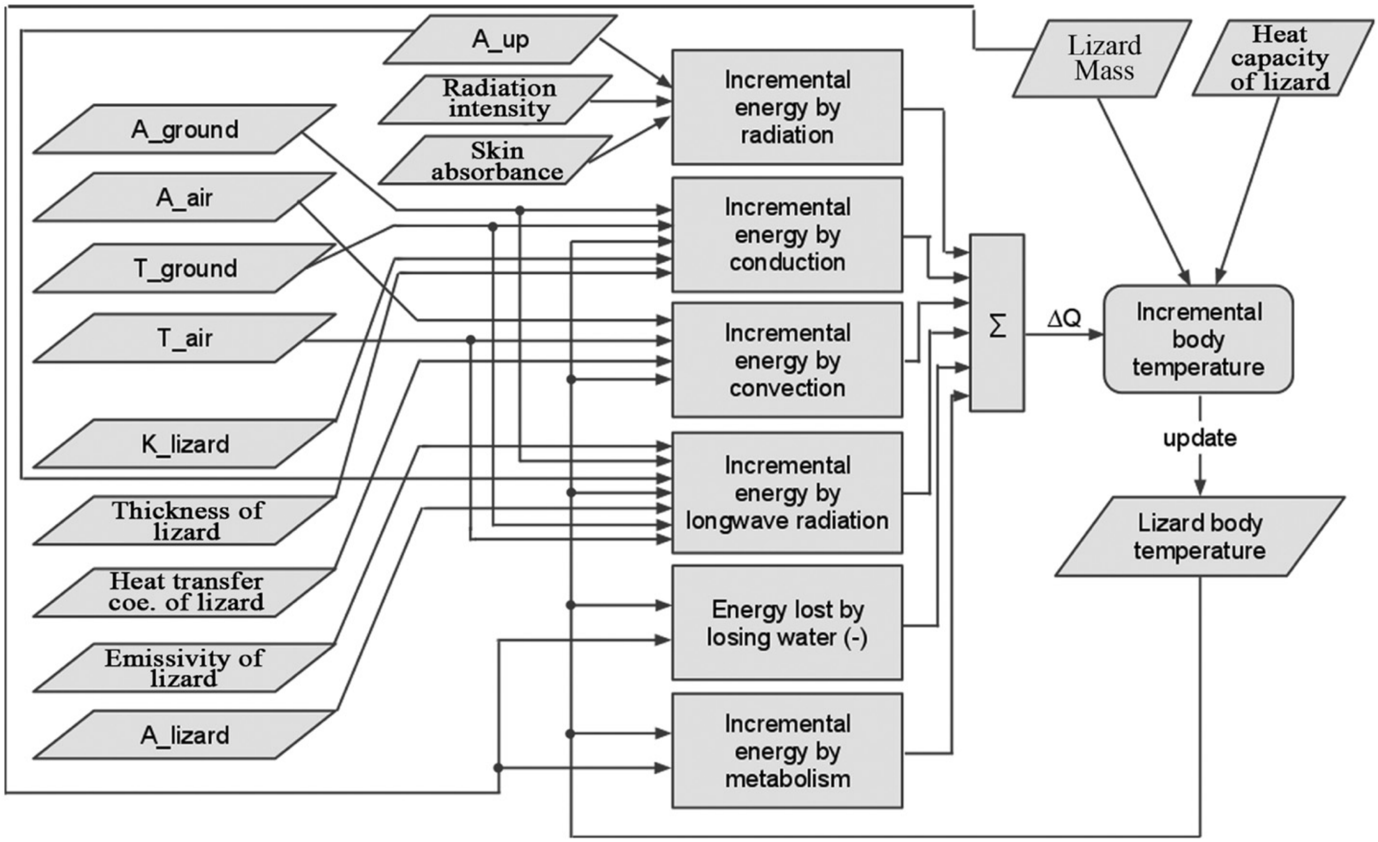

Fig. 1. Lizard's body temperature dynamics, decided by thermal environment and physiological parameters. A_lizard, A_ground, A_air, and A_up stand for the total area of the target lizard, the area that the lizard contacts with the ground, the area the lizard exposes in the air and the projection area of the lizard, respectively; T_ground, T_air represents the ground temperature and the air temperature of the thermal environment in Celsius, respectively.

uses the above formulas derived from desert iguanas, since the two lizards have similar body size and live in relatively similar environments.

2.2. Body temperature simulation

With the quantification of the lizard's energy budget, the dynamic changes of body temperature under changing thermal conditions can be modeled by

$$\Delta T = \frac{\Delta Q_e}{M_{lizard} c_{lizard}} \tag{9}$$

where ΔT is the body temperature changes in a certain period of time, ΔQ_e is the net energy received within that time, M_{lizard} stands for the mass of the lizard in unit of kg, and c_{lizard} represents the specific heat capacity of the animal.

An estimation of the specific heat capacity of 3762 J kg^{-1} of a lizard (c_{lizard}) was made by Porter et al. (1973). This value was adopted to calculate the body temperature change in a fixed time interval. The numerical model was implemented with Simulink®, iterating by a 10-s fixed time step. Fig. 1 details the model as a diagram, and specifically shows how parameters and heat transfer terms are connected and how the energy exchange leads to the dynamic balancing of the body temperature of lizard.

3. Model evaluation

3.1. Experimental design

Timon lepidus (Ocellated lizard) was chosen as the target animal for developing the model as it is widely studied and the model may be parameterized. It is a ground-dwelling lizard that is widely distributed in Spain, Portugal, southern France and northwestern Italy. The skin color of an adult has a camouflaged effect comprising mottled blue, green and brown patches interspersed with brighter spots. In the wild, it feeds on insects, snails, newly hatched birds and fruits (Pleguezuelos et al., 2008).

3.1.1. Terrarium configuration

An experiment was carried out at a reptile zoo "Dierenpark De Oliemeulen" during September, 2008 in Tilburg, the Netherlands. A glass terrarium of size 245 cm × 120 cm × 115 cm was constructed. At the bottom of the terrarium, at least 10 cm of gravel and sand were mixed to form a flat substrate surface. Photoperiod was maintained at 14L:10D with a 100-W heat lamp. An infrared heat lamp of 100 W provided additional heat input for 5 h during the middle of the photophase. A 4-year-old male *Timon lepidus* was kept in the terrarium for 10 day before the experiment started, in order that the lizard could acclimatize to the new environment. The lizard was fed on vegetables, crickets, newly born mice, and some fruits such as apple and banana.

Traditionally, the body temperature of lizards is measured by a contact thermometer that reads the cloacal temperature, or by an inbuilt data logger and radio transmittance device implanted inside the lizard's body (Kerr et al., 2008). In this study, however, thermal infrared imagers were used that read the body temperature remotely. This approach has three main advantages: Firstly, it measures the body temperature without physical contact with the lizard, so the measurements were not affected by the changing metabolic rate as a response of struggling. Second, the thermal imagers measured also the surface temperature of the substrate, based on which the conductive energy exchange between animal and the ground could be calculated. Thirdly, the animal was not handled or stressed in any way by the measurement process. Three IRISYS® 1011 thermal imagers were mounted in a row at 2 m above the bottom of the terrarium, pointing down with their field-of-views (FOVs) covering a continuous rectangular area of the bottom (33 cm × 100 cm).

3.1.2. Data collection

During the experiment, the brightness temperature (i.e., the temperature of a black body when emitting an equivalent amount of radiation) of both the lizard and the land surface were measured by the IRISYS 1011 thermal imagers. The land surface temperature just beneath the lizard was interpolated from the measurements of the surrounding 8 pixels. The air temperature was recorded by "Hobo™ Temperature Smart Sensors" placed at the height of the lizard; and the full spectrum radiation within the terrarium was mapped by "Hobo™ Silicon Pyranometer Smart Sensors". Some researchers argued that the skin absorbance (α_L) of some lizards co-varied with the body temperature, especially when the body temperature is higher than 38 °C (Norris, 1965; Porter, 1967), while other studies consider it constant (Waldschmidt and Tracy, 1983a). Therefore, to determine whether the reflectance of the lizard skin varied with the body temperature, we used a FieldSpec-3 spectrometer (ASD, Boulder, USA) to measure the spectral reflectance of the target lizard under two different body temperatures. 20 spectra were measured at body temperatures of 36 °C and 40 °C, respectively, followed by a *t*-test to determine whether there was a significant difference on the skin reflectance of target species at different body temperatures (Table 1).

3.2. Calibration of the body temperature model

The lizard body temperature model has 6 input variables and 9 parameters (Table 2). The input variables were directly measured while the parameters were received from the literature (standard parameterization). To further improve the performance of the model and generate realistic parameters (improved parameterization), we re-estimated the model parameters using a Monte Carlo simulation.

Table 1
Details of the data collection of the experiment.

Variable	Unit	Spatial resolution	Recording interval	Device	Accuracy (*specified by the manufacturer)
Lizard surface temperature	°C	4.4 cm^2	10 s	IRISYS 1011 thermal imager	± 0.3 K
Ground surface temperature	°C	4.4 cm^2	10 s	IRISYS 1011 thermal imager	± 0.3 K
Air temperature	°C	–	10 min	Temperature and RH smart sensor	± 0.7 K
Full spectrum radiation	$W^2\ m^{-2}$	Interpolated to 4.4 cm^2	–	Hobo™ Silicon Pyranometer smart sensor	± 15 $W^2\ m^{-2}$
Skin spectral reflectance	–	–	Spectral resolution: 3.5 nm at 700 nm	ASD FieldSpec® 3 spectrometer	–

Table 2
Input parameters ranges setting for the look-up table.

Parameters	Measured/ estimated	Symbol/unit	Ranges setting for parameter adjustment
Lizard mass	M	m_{lizard} (kg)	0.19
Land surface temperature	M	T_{earth} (K)	297.15
Air temperature	M	T_{air} (K)	297.65
Initial lizard skin temperature	M	T_{skin} (K)	303.15
Radiation intensity	M	Q_{solar} ($\mathrm{W\,m^{-2}}$)	300
Skin absorbance	M	–	0.936
Lizard specific heat capacity	E	C_{lizard} ($\mathrm{J\,K^{-1}\,g^{-1}}$)	3.762 ± 0.37
Lizard thickness	E	δ (m)	0.015 ± 0.0015
Thermal conductivity	E	K_{lizard} ($\mathrm{W\,K^{-1}\,m^{-1}}$)	0.502 ± 0.050
Convection coefficient	E	h_L ($\mathrm{W\,m^{-2}\,K^{-1}}$)	10.450 ± 1.045
Lizard Area	E	A_L ($\mathrm{m^2}$)	0.032 ± 0.003
Contacting area with the earth	E	A_{down} ($\mathrm{m^2}$)	0.003 ± 0.0003[a]
Projected lizard area	E	A_p ($\mathrm{m^2}$)	0.013 ± 0.001
Emissivity of lizard skin	E	–	0.950 ± 0.1
Emissivity of land surface	E	–	0.950 ± 0.1

[a] The A_{down} is centered on $0.4A_L$ as the lizard kept lying flattened when measuring.

In a preliminary step, the 9-dimensional parameter space was sampled over an equally distributed grid. Across each parameter's range, which was assumed to be ±10% of its reference value, the body temperature model was run at each sample point using the input of the actual thermal environment of the animal experiment, thereby predicting the range in body temperature over time. Meanwhile, the observed lizard body temperature dynamics were recorded, and later compared with the predicted values.

Specifically, the calibration used the root mean square error (RMSE) to compute the deviation between the observed body temperatures and predicted temperatures. The parameter combination by which the prediction had the lowest RMSE was selected, allowing the bio-physical parameters of the lizard to be determined from the body temperature observations.

3.3. *Validation of the body temperature model*

Independent observations ($N=31$) of lizard's body temperature were collected to validate the body temperature model. These data were chosen based on two criteria: (1) continuous body temperature records when the lizard was moving within the field of view of the thermal imagers; and (2) while within the field of view, both heating and cooling phases were experienced by the lizard. The observations were compared with model simulations and the root mean square error (RMSE) of the temperature prediction was calculated.

3.4. *Sensitivity analysis of the body temperature model*

As a method to test the robustness of the model, sensitivity analysis is necessary as it examines how different values of independent variables will impact the result (Chinneck, 2004), which is the body temperature of the lizard in this case. We analyzed how a change in each input variable affects the body temperature prediction after 1 and 10 min. The sensitivity of the model was estimated by increasing and decreasing each input parameter by 10% from its typical value, while leaving the other input variables constant. The testing thermal environment was: ground temperature of 24 °C, air temperature of 24.5 °C, radiation intensity of 300 $\mathrm{W^2/m^2}$, and the initial lizard body temperature of 20 °C.

4. Results

4.1. *Absorbance of the lizard's skin*

In the 40 measurements, the skin absorption varied little and did not show significant difference at different body temperatures. Fig. 2 shows the spectral absorption curve of the lizard's skin. The spectral reflectance showed that there was no significant effect of lizard body temperature on absorbance (t-test, $n=40$, $p=0.139$, $\alpha=0.05$). Therefore, we consider α_L to be a constant value of 0.936.

4.2. *Calibration of the body temperature model*

After improved parameterization, the root mean square error (RMSE) of the predicted body temperature was 0.44 °C, when the body temperature rose from 26.40 °C to 31.40 °C (Fig. 3a), while the RMSE was 0.24 °C when the body temperature dropped from 33.9 to 32.0 °C (Fig. 3b). However, with the standard parameters received from the literature, the RMSE values of the predicted body temperature were 4.19 °C (rising temperature) and 0.79 °C (temperature drop), respectively.

4.3. *Validation of the body temperature model*

The independent dataset ($N=31$) of the measured lizard body temperatures was used to validate the calibrated model. To avoid biased results, a period in which the lizard experienced both heating and cooling phases was chosen. The model performance may be visually compared in Fig. 4a before and after the parameterization when using the independent validation dataset. Fig. 4b illustrates the model performance with the improved parameters in term of RMSE: after the calibration, the RMSE of temperature prediction decreased from 1.35 °C to 0.59 °C.

4.4. *Sensitivity tests of the body temperature model*

Sensitivity tests were performed to determine how responsive the body temperature change is to each of the parameters we estimated for the representative lizard we have chosen. Fig. 5

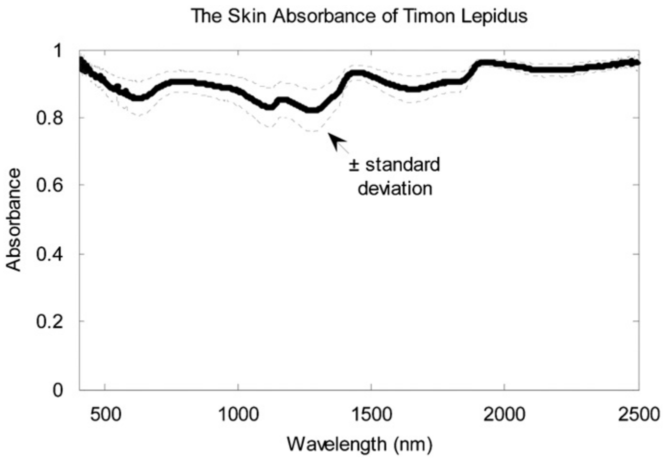

Fig. 2. The spectral absorbance of the *Timon lepidus'* skin in 40 spectral measurements, showing mean value (solid line) and standard deviation (dotted lines).

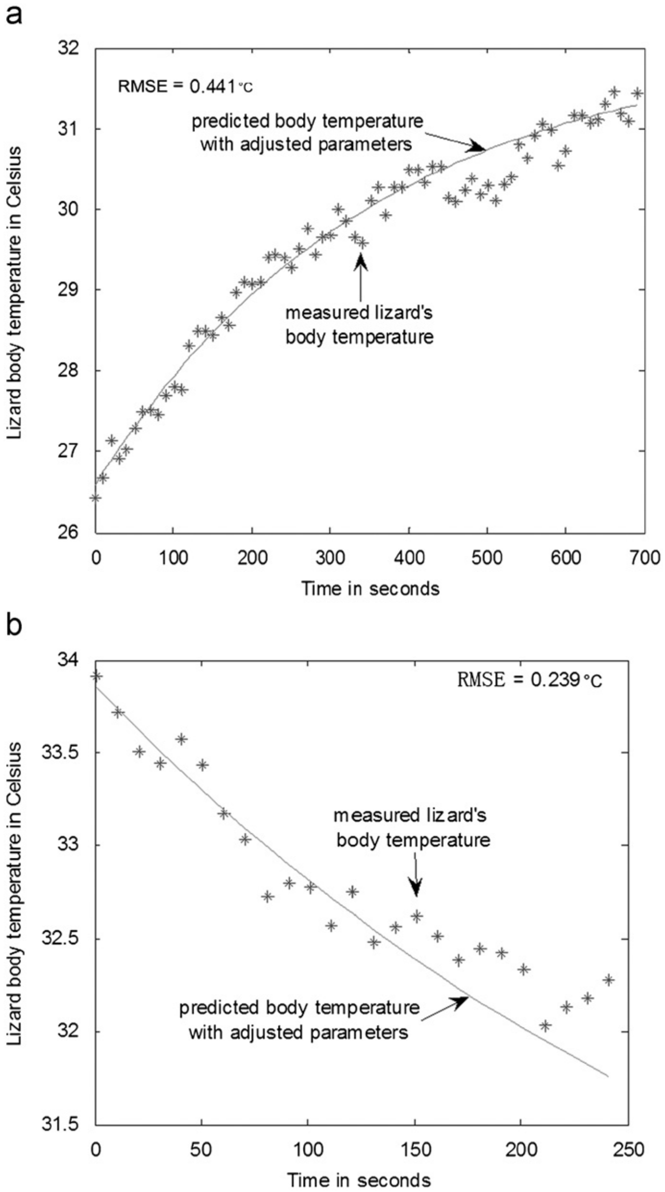

Fig. 3. (a) Model parameterization: the predictions made by the body temperature model with the best parameters fitting training data of a basking lizard. (b) Model parameterization: the predictions made by the body temperature model with the best parameters fitting training data of a cooling lizard.

shows how each input variable affects the body temperature prediction during the following one minute. In addition to the initial body temperature, the air temperature and ground surface temperature had important influences on the body temperature of the lizard. Direct radiation intensity was relatively less sensitive compared with the above two thermal parameters.

Fig. 6 shows how each input variable affects the body temperature prediction for the following 10 min. This time, the ground surface temperature and air temperature dominate the final body temperature of lizards, while the initial body temperature has no effect. In addition, a 10% increase in radiation intensity or skin absorbance can raise the body temperature by 2% within 10 min, which means the final body temperature is also sensitive to the radiation received.

It can be noted that the response of three variables (convection coefficient, lizard area and lizard emissivity) change direction between the 1-min test and the 10-min test. It is because in the most of the time within the 1-min test, the lizard was colder than the environment. As a result, energy transferred from the

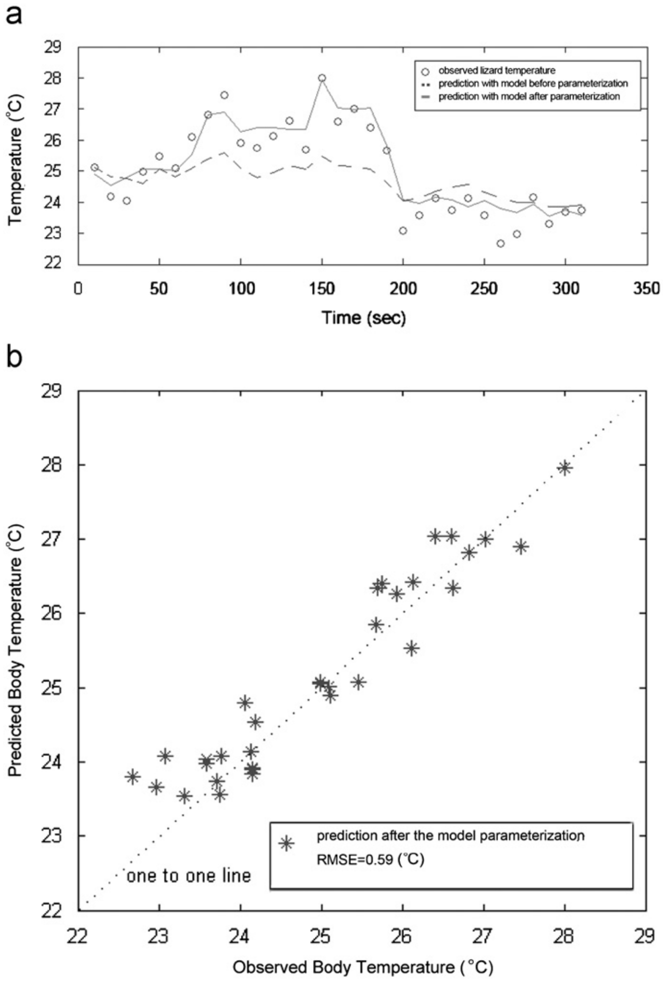

Fig. 4. (a) The comparison between the prediction errors of the body temperature model before (dotted line) and after (solid line) parameterization. (b) The observed body temperature vs. the predictions of the calibrated model, model validation using independent dataset.

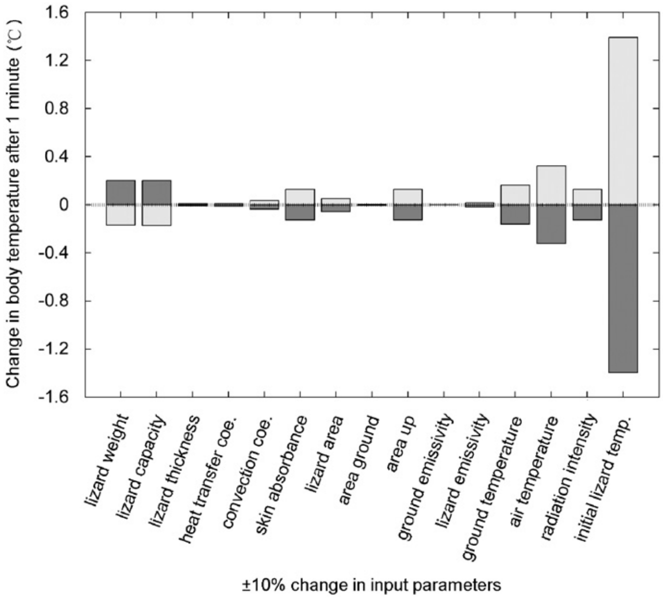

Fig. 5. The sensitivity of lizard body temperature responding to input parameters: one-min test. Each parameter is increased and decreased by 10% from its estimated value, while leaving the other inputs constant. Lighter colored bars illustrate the results of increasing the parameters; darker colored bars represent the results of decreasing the parameters.

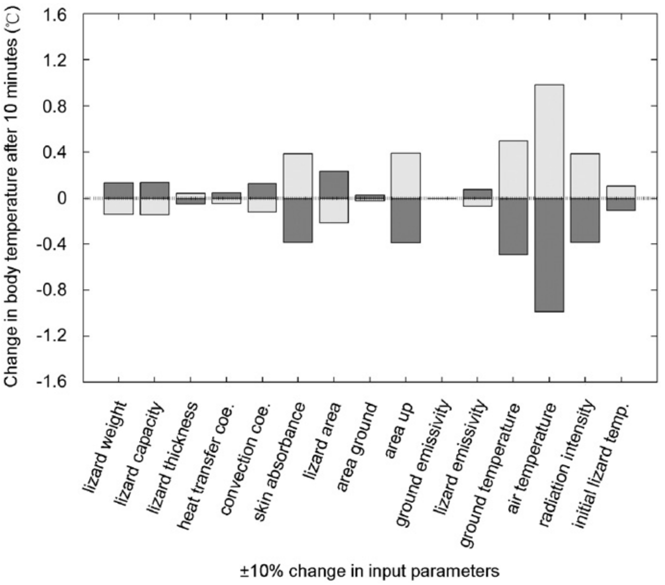

Fig. 6. The sensitivity of lizard body temperature responding to input parameters: ten-min test. Each parameter is increased and decreased by 10% from its estimated value, while leaving the other inputs constant. Lighter colored bars illustrate the results of increasing the parameters; darker colored bars represent the results of decreasing the parameters.

environment to the animal through conduction, convection and long-wave radiation had a positive impact on the temperature of the lizard, so higher values of these variables (meaning faster exchange rate of energy) led to a higher final body temperature; while in the 10-min test, as the lizard soon got warmer than the environment, so the energy transferred from the animal to the environment had a negative impact on the body temperature of the lizard. As a result, a higher value of these variables led to a lower final body temperature.

5. Discussion

With a bio-physical model, we predicted the transient body temperature of a lizard, *Timon lepidus*, in response to the thermal environment. In this model, six heat transfer terms were taken into account: solar radiation, convective heat flow, longwave radiation, conductive heat flow, metabolic heat gain and respiratory energy loss. The instantaneous values of these terms were calculated from the thermal environment and the parameters of the target animal, namely, body mass, size, skin absorbance, specific heat capacity, conductive heat transfer coefficient, convection coefficient and surface area. We estimated some heat related bio-physical parameters that were difficult to measure in-situ by using a Monte Carlo simulation on the basis of reference values obtained from literature. As a result, the accuracy of the body temperature prediction was improved. Before the parameter estimation, the RMSE of the body temperature prediction was 1.35 °C; while after, it dropped to 0.59 °C. The results of the study showed that the body temperature model with the Monte Carlo parameterization technique presented here can accurately reflect the body temperature dynamics of lizards confined in a laboratory condition.

The ground surface temperature and air temperature are the two environmental factors to which the body temperature of a lizard appears to be most sensitive. Although many bio-physical models have accounted for the heat exchange between an animal and the substrate (O'Connor and Spotila, 1992; Tracy, 1976), in practical terms, the thermal characteristics of the ground surface often vary substantially and are difficult to measure in the field (O'Connor and Spotila, 1992). In this study, the successful application of the thermal infrared imagers with considerate spatial interpolation offered a new approach to monitor the thermal landscape accurately and remotely. According to the observation of the study, the heat transfer term of the metabolic energy gain did not entirely offset the evaporative energy loss, as some studies suggested (Bartholomew, 1982; Tracy, 1982). Therefore, ignoring or inaccurately measuring them may have a negative impact on the prediction accuracy of the model. For example, if the three terms of conduction, metabolic gain and evaporative loss are ignored, the model RMSE increases from 0.59 °C to 0.85 °C.

It can be noted in Fig. 3a, that at around 500 s, the model slightly overestimated the lizard's temperature. To explain this phenomenon, the experimental records were checked. We found that the lizard was curled up during this period, so the temperature of the body and the cooler tail was possibly mixed in one thermal infrared pixel. It is reasonable that the value of the mixed pixel is therefore lower than the actual body temperature. We also noted that the lizard cools at a slightly slower rate than predicted (Fig. 3b after 150 s), though this phenomenon has been previously noted (Bartholomew, 1982; Bartholomew and Lasiewski, 1965). A possible reason may be attributed to circulatory shutdown in the appendages (Porter et al., 1973). When cooling, a lizard may slow down the blood flow rate in the appendages by vasoconstriction to conserve energy (Dzialowski and O'Connor, 1999, 2004).

For the independent dataset, the model gave an unbiased body temperature prediction with RMSE of 0.59 °C (Fig. 4b). It was suspected that there were three possible sources causing this error, i.e., the inaccurate measurement of the environment, the simplification of the model, and the parameterization of the model. For the measurement of the environment, the convection is difficult to characterize accurately, especially due to the turbulent flows from environment (Vogel, 1981). The contact area between land surface and the lizard was also difficult to measure and could only be assumed in this study. The radiation was not always perpendicular to the land surface, but also from the side, which may have an impact on the amount of radiation received by lizards. This possible source of error was not considered in this study. Regarding the model structure, the model description of the heat transfer processes was simplified, but the heat fluxes are complex. We assumed that all heat transfer coefficients were static, such as the convection heat transfer coefficient, while in reality, coefficients are simple empirical approximations for complex heat exchange processes. Determining the coefficients under one set of conditions and applying them under another may be a source of error (O'Connor and Spotila, 1992). Assumptions about the target animal also allowed a simplification of the model: The body shape of the animal was assumed to consist of a series of cylinders—one for the main body and six for the appendages, as O'Connor (1999) proposed. However, the diversity in the shape of lizards may introduce error when estimating surface area as well as to the heat transfer terms, thereby weakens the predictive ability of the model. The energy loss attributed to the passing of feces and urine, the rapid temperature rise after food intake (Clark et al., 2006), and the energy consumption through activity were not considered in our model, but could be added. In addition, a thermally homogeneous object was used to represent the target species, while the heat transfer inside the body is far more complex (Dorcas and Peterson, 1997; Georges, 1979), even the surface temperature distribution of the lizard is not always homogeneous. Some multi-layered models considered the different conductivities and positions of the animal components, such as flesh, bones, fat, blood and skin (Porter and Gates, 1969; Porter et al., 1973; Tracy, 1976). However, such models require more detailed data about the animal than that is normally available (O'Connor and Spotila, 1992). As for the parameterization process, previous studies have shown that parameter optimization may lead to equifinality, i.e., models with different parameters all lead to acceptable results when the information content in calibration data is not in balance with the model complicity (Mitchell et al., 2009). This is the inborn limitation of this parameter retrieval method. To reduce this effect, we firstly made use of prior knowledge from literature to determine the rough values of the parameters, and then validated the model using data from both heating and cooling phases of the lizard. With these efforts we expected to pinpoint parameters and to diminish the possibility of error-posting. Despite all of these errors, because the experiment was carried out in a terrarium, many environmental factors such as wind speed, air temperature, substratal surface temperature and radiation were constant or controlled or have been carefully recorded, leading to a satisfactory accuracy of body temperature prediction.

However, to test the performance of the body temperature model in the field, by up-scaling the experiment to a natural lizard's microhabitat, challenges emerge through variation in environmental factors, as well as measurement limitations imposed by the instrumentation. At field scale, topography and vegetation cover may not be homogenous, and radiative energy received by the animal consists of direct and indirect radiation in the open area. As a result, additional field data such as the slope and aspect of the habitat, the vegetation cover, the canopy density, and the diffuse sunlight has to be considered to calculate the actual radiative energy received. Because different land covers have different emissivity, an emissivity map of substrate has to be estimated for a correct retrieval of ground surface temperature, to get ipso facto an accurate calculation of conduction. The wind speed at the height of a lizard has to be measured in-situ because in the field wind will dramatically affect the convection. Also the feeding activities need to be noted because the body temperature is significantly lower when fasting than after feeding (Wang et al., 2002) (contrary to in our laboratory conditions where food was always available). In addition, as there is no hard boundary of lizard's home range, it is expected that the animal will live across a much larger territory. In order to record the ground surface temperature dynamics for a much wider area, the thermal infrared imager should have a much higher spatial resolution to ensure that pure pixels of 'lizard' can be recorded so the body temperature of the animal can be retrieved accurately. Despite all the difficulties, the model used in this study is physically based and therefore has the ability to cope with field situations when parameterized by the Monte Carlo method presented in this paper.

6. Conclusion

This paper described a bio-physical model for body temperature simulations and the use of a Monte Carlo techniques to refine model parameters based on reference values from the literature. In conclusion, the transient body temperature of an ectotherm was modeled accurately from its thermal environment in a laboratory setting. The model inversion technique for the retrieval of thermal characteristics of the animal from continuous body temperature observation clearly enhanced the accuracy of temperature prediction. Although it was not the scope to test the body temperature model and the calibration techniques in a field environment, the model due to its physical nature has the potential to work under field condition, proper model parameterization provided. Up-scaling the model to a real lizard habitat under natural conditions will be the scope of following research activities that will build on the presented work.

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