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Heat Transfer in a Microvascular Network: the Effect of Heart Rate on Heating and Cooling in Reptiles (*Pogona barbata* and *Varanus varius*)

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Thermally-induced changes in heart rate and blood flow in reptiles are believed to be of selective advantage by allowing animal to exert some control over rates of heating and cooling. This notion has become one of the principal paradigms in reptilian thermal physiology. However, the functional significance of changes in heart rate is unclear, because the effect of heart rate and blood flow on total animal heat transfer is not known. I used heat transfer theory to determine the importance of heat transfer by blood flow relative to conduction. I validated theoretical predictions by comparing them with field data from two species of lizard, bearded dragons (*Pogona barbata*) and lace monitors (*Varanus varius*). Heart rates measured in free-ranging lizards in the field were significantly higher during heating than during cooling, and heart rates decreased with body mass. Convective heat transfer by blood flow increased with heart rate. Rates of heat transfer by both blood flow and conduction decreased with mass, but the mass scaling exponents were different. Hence, rate of conductive heat transfer decreased more rapidly with increasing mass than did heat transfer by blood flow, so that the relative importance of blood flow in total animal heat transfer increased with mass. The functional significance of changes in heart rate and, hence, rates of heat transfer, in response to heating and cooling in lizards was quantified. For example, by increasing heart rate when entering a heating environment in the morning, and decreasing heart rate when the environment cools in the evening a *Pogona* can spend up to 44 min longer per day with body temperature within its preferred range. It was concluded that changes in heart rate in response to heating and cooling confer a selective advantage at least on reptiles of mass similar to that of the study animals (0.21–5.6 kg).

1. Introduction

In one of the central paradigms in the field of thermal physiology of ectothermic vertebrates, changes in blood flow are thought to enable reptiles to control heat transfer between their body core and the environment (Bartholomew, 1982). It has been shown that cool lizards entering a heating environment, while basking in the morning for example, increase their heart rate while warming. Conversely, warm lizards entering a cooling environment, entering shade after basking for example, decrease their heart rate. Hence, at any given body temperature (T_b), heart rate during heating is significantly faster than during cooling, and this heart rate "hysteresis" has been demonstrated to occur in the laboratory (Bartholomew & Tucker, 1963) and in the field (Grigg & Seebacher, 1999). Changes in heart rate have been shown in elicit proportional changes in peripheral blood flow (Grigg & Alchin, 1976;

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Smith, 1976; Robertson & Smith, 1979), and it is thought that the capacity to change peripheral blood flow is of selective advantage because it allows reptiles to remain warm for longer during the day by increasing rates of heating in the morning and decreasing cooling rates in the evening (Bartholomew, 1982).

Despite the fact that the notion of heart rate and blood flow "hysteresis" has become firmly entrenched in our thinking of reptile thermal relations as a physiological means of thermoregulation, it is not known if, or by how much, blood flow contributes to total heat transfer within the body. There is circumstantial evidence that blood flow augments total rates of heating and cooling in the observations that dead animals heat and cool significantly slower than live ones (Bartholomew & Tucker, 1963), but these observations do not reveal the underlying mechanism. Here I present a theoretical analysis of heat transfer by blood flow in a microvascular network (Fenton & Zweifach, 1981; Dawant *et al*., 1986) which details the importance of blood flow relative to heat exchange by conduction between the animal surface and core. It was my aim to determine if heat transfer by blood flow was of functional significance in thermoregulation of free-ranging lizards. For example, if rates of conductive heat transfer between the animal surface and core were substantially greater than the rate of heat transferred by blood flow, it would be doubtful if changes in blood flow and heart rate really represent a selective advantage. Also, it may be that the functional significance of blood flow varies in animals of different size and/or species (Grigg *et al*., 1979; Turner & Tracy, 1985a). Hence, I measured heating and cooling in two differently sized species of lizard, bearded dragons (*Pogona barbata*, 0.21–0.59 kg) and lace monitors (*Varanus varius*, 4.00–5.60 kg), which also allowed me to validate and compare predictions from the independently derived theoretical analysis to field data.

Blood flow through the arterioles, capillaries and venules that make up microvascular networks in vertebrates is also of more general physiological and medical interest, because of its importance in determining blood pressure and oxygen transport (Sharan *et a*l., 1998). Oxygen transport and heat transfer may be functionally connected because of the temperature dependence of the blood oxygen dissociation curve, so that insights into heat transfer in microvascular networks may also lead to a better understanding of its oxygen transport characteristics.

2. Materials and Methods

2.1. FIELD DATA

Bearded dragons ($N = 6$), *Pogona barbata*, were captured by hand in south-east Queensland, Australia. Heart rate, body temperature (T_b) and, whenever possible, behaviour were monitored in a large outdoor enclosure (c. 100 × 50 m) near Brisbane (27°4′ S, 153°2′ E) which contained natural bushland. Each animal was monitored for 8–11 days and then released at its capture site. Lace monitors ($N = 6$), *Varanus varius*, were hand-captured on a sheep property near Texas, Queensland (28°46′ S, 151°4′ E). Each animal was monitored for 4–13 days before being released at its capture site.

T_b was measured with surgically implanted temperature-sensitive radio transmitters (Sirtrack, Havelock North, New Zealand), which were encased in non-reactive epoxy resin and weighted 10–15 g depending on the size of the battery. Transmitters were implanted into the peritoneal cavity of locally anaesthetized animals (using Lignomav), among the internal organs. Before implantation, transmitters were calibrated in a temperature-controlled water bath and were accurate to 0.1°C. T_b was determined every 5–10 min by measured the temperature-dependent time intervals between two transmitter signals with a digital processor (Telonics, Pasadena, U.S.A.) connected to a telemetry receiver (Telonics, Pasadena, U.S.A.).

Heart rate was also measured telemetrically, and transmitters were taped to the base of the lizard's tail just posterior to the vent. Heart rate transmitters (Sirtrack, Havelock North, New Zealand) were encased in epoxy resin and had two external contact points for electrode attachment, and their maximum sensitivity was 90–100 μV. Plastic-coated surgical steel wire was used for electrode leads with 10–15 mm of the insulation removed to expose bare wire at the active end. Using a straight surgical needle, one electrode was passed under the loose skin from the transmitter to a position ventral to the heart where it was sutured in place. The other electrode was sutured under the skin at the base of the tail. All heart rates reported here were measured on stationary, resting animals because heart rates could not be measured when lizards were moving due to electrical interference from muscle contractions (see also Grigg & Seebacher, 1999).

Heart rates were compared by analysis of variance with Species, Mass and Heating/Cooling as factors, and T_b as a covariate. Data sets for each lizard were randomized and then subsampled, and 30 random data points per lizard were used as replicates in the analysis.

Environmental conditions were monitored with sensors connected to a datalogger (Data Electronics, Melbourne, Australia). Air temperature was measured in the shade (with an LM 335 semiconducter) 1 m above the ground, and ground temperature was measured on a bare patch of ground with the sensor (LM 335) lightly covered with soil. Solar radiation was measured with either a tube solarimeter (Irricrop Technologies, Narrabri, Australia) or a pyranometer (Sol-Data 80HDX, Silkeborg, Denmark), and wind speed was measured with an anemometer (Pacific Data Systems, Brisbane, Australia). Operative environmental temperatures were calculated by solving a steady-state energy balance equation (Bakken & Gates, 1975; Tracy, 1982; Seebacher, 1999).

2.2. THEORETICAL ANALYSIS

Following recommendations by O'Connor & Spotila (1992), I formulated the theoretical model in the simplest possible configuration, with the proviso to refine it should model predictions prove to be inadequate when validated against field data. Hence, I made two assumptions which simplified the calculations. Firstly, I assumed that lizards could be represented by an infinite cylinder without appendages. I estimated the dimension of cylinders from morphometric measurements of the study animals. Appendages are likely to be important only if blood was shunted between them and the torso, so that blood flow rates were significantly different in the appendages compared to the torso (Dzialowski & O'Connor, 1999), or if appendages experienced significantly different operative temperatures compared to the torso, for example if animals submerged their legs into water, which was not the case in this study. Moreover, the assumption that T_b is regulated by blood flow to the appendages is speculative as there are no experimental data suggesting that blood flow to the appendages is in any way regulated differently from that of the torso. There are, however, ample data in the literature demonstrating that reptiles control blood flow to the body surface, and that varying blood flow rates are proportional to changes in heart rate (Morgareidge & White, 1972; Grigg & Alchin, 1976; Bartholomew, 1982). Therefore, I restricted my calculations to heat transfer as a function of changes in blood flow to the periphery of the torso.

Secondly, I assumed that the total heat exchange occurring in the microvascular network contributes to the change in T_b. This ignores possible heat transfer between tissue and vessels transporting blood between the microvascular network and the core. Furthermore, there may be counterflow heat exchange between arterial and venous vessels within the microvascular network when these are arranged in parallel (Bejan, 1982). Both the latter phenomena may influence temperature gradients and heat transfer within the body, although O'Connor (1999) surmised that heat transfer from tissue across the wall of blood vessel and hence to the core is negligible compared to other avenues of heat transfer. I felt, therefore, that the mathematical complexity required to adequately address these issues would detract from the biological questions asked here, but it may well be worthwhile to explore this potential "fine tuning" of heat transfer in a future study.

2.3. CONDUCTION

Conduction between the body surface and core was calculated by non-dimensionless analysis for an infinite cylinder (Carslaw & Jaeger, 1995; Incropera & DeWitt, 1996). The initial heat equation is

$$\partial^2 \theta / \partial r^{*2} = \delta \theta / \partial Fo, \tag{1}$$

where θ is the dimensionless temperature $(T_b - T_e)/(T_i - T_e)$ with T_e being the operative environmental temperature (Bakken & Gates, 1975), T_i the initial T_b, r^* a spatial coordinate (r/L, where r is the radius, and L the length of cylinder) and Fo the Fourier number ($Fo = \alpha t/r^2$ where α is the thermal diffusivity and t the time). The above equation has a series solution for the cylinder midline temperature (Schneider, 1955)

$$\theta_0 = \sum C_n \, e^{(-\zeta_n^2 Fo)}, \tag{2}$$

where the coefficient

$$C_n = 2/\zeta_n [J_1(\zeta_n)/\{J_0^2(\zeta_n) + J_1^2(\zeta_n)\}] \tag{3}$$

and ζ_n are the positive roots of the transcendental equation

$$Bi = \zeta_n [J_1(\zeta_n)/J_0(\zeta_n)] \tag{4}$$

with Bi being the Biot number (Incropera & DeWitt, 1996). The series solution of the Bessel functions (Piaggio, 1965), J_0 and J_1, were evaluated for the first five roots of ζ_n (Anonymous, 1958), and the series converged after 25 terms.

Convection coefficients (h) used to calculate the Biot number ($Bi = h \cdot r/k$) were determined by methods given in Mitchell (1975), and the conductivity of tissue (k) was assumed to be 0.5 W m^{-1} K^{-1} (Bowman *et al.*, 1978).

2.4. CONVECTION IN A MICROVASCULAR NETWORK

Heat transfer by blood flow was assumed to occur via a microvascular network under the skin surface (Fig. 1). Peripheral microcirculation was represented by a branching network consisting of two parts, arterial and venous, which are connected at the level of the smallest segments (capillaries) (Horton, 1945; Fenton & Zweifach, 1981; Dawant *et al.*, 1986). The topography of each network is defined by the number of the smallest segments, capillaries, per unit area which determine the number of the next largest segments, and so on, according to established bifurcation ratios ($RB = 2.65$ for the arterial network and $RB = 2.80$ for the venous network; Dawant *et al.*, 1986). Length and diameter of segments at each branching level are determined by the ratios

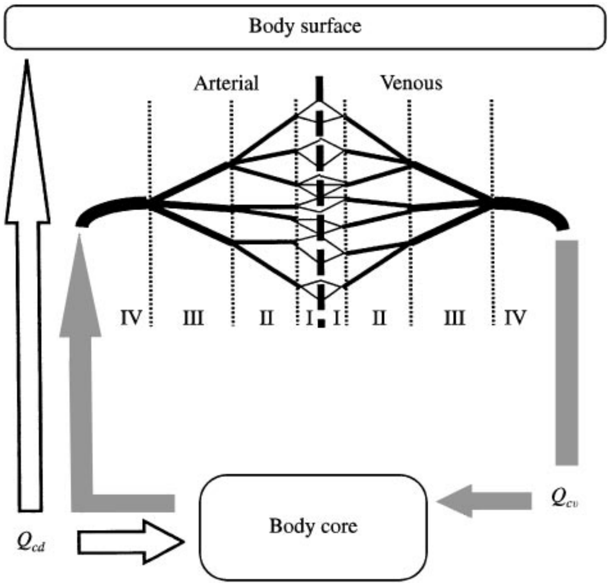

FIG. 1. Schematic representation of heat transfer in a lizard. Heat is transferred between the microvascular network, which is located just beneath the body surface, and the body core via blood flow (Q_{cv}). The microvascular network is composed of an arterial and a venous part, each of which consists of a branching network, and the two are connected at the level of the smallest ducts (capillaries, I). The number of perfused vessles of different diameter (order) depends on the blood flow rate, and four orders are shown in each branching network here. Furthermore, in the analysis, heat transfer in the microvascular network is three-dimensional but, for the sake of clarity, the network is shown two dimensionally. Heat exchange between the body surface and the core occurs also by conduction (Q_{cd}).

$$RD_j = D_{j+1}/D_j \tag{5}$$

and

$$RL_j = L_{j+1}/L_j, \tag{6}$$

where D_j and L_j are diameter and length, respectively, at branching order j (Horton, 1945; Fenton & Zweifach, 1981). The diameter and length of capillaries were 10 and 1000 μm, respectively (Honig *et al.*, 1977; McDonald, 1998). $RD_j = 1.25$ for arteries and 1.50 for veins, and $RL_j = 1.30$ for arteries and 1.40 for veins (Dawant *et al.*, 1986). Furthermore, it was assumed that the arrangement of the total network is three-dimensional with each branching order arranged in a plane. The plane of the smallest segments lies closest to the skin surface, and each consecutive plane of larger segments is separated from the foregoing plane by the length of the smaller segments.

Blood flow (Q, $\mathrm{m^3\,s^{-1}}$) in each segment was calculated according to Poiseuille's law

$$Q = \pi (P_1 - P_2)\, r^4 / 8\eta l, \tag{7}$$

where $P_1 - P_2$ is the pressure difference between two segments of different order, r is the segment radius, and η the blood viscosity ($1300\ \mathrm{kg\,s^{-1}\,m^{-1}}$) (Berne & Levy, 1997). Assuming steady flow of an incompressible fluid, blood pressure (P, N) was calculated using a form of Bernoulli's equation

$$P_2 = P_1 + 0.5\,\rho\,(v_1^2 - v_2^2), \tag{8}$$

where ρ is the density ($1000\ \mathrm{kg\,m^{-3}}$), v the velocity ($\mathrm{m\,s^{-1}}$) which is defined by $A_1/v_1 = A_2/v_2$ with A being the cross-sectional area (Halliday & Resnick, 1978; Wood, 1999).

Capillary density changes with body mass to the power of -0.083 (West *et al.*, 1997), and the number of open, perfused capillaries per unit area increases with metabolic rate in mammals (Schmidt-Nielsen & Pennycuik, 1961). Furthermore, Schmidt-Nielsen (1975) reported that density of perfused capillaries changes from 100 $\mathrm{mm^{-2}}$ in an inactive guinea pig to 3000 $\mathrm{mm^{-2}}$ when the animal was active. There are no comparative data for reptiles, so that the following assumption was made to estimate the capillary density of reptiles from data reported for mammals. Values for guinea pigs were scaled down to a reptilian metabolism by assuming that the metabolic rate of guinea pigs is five times higher than that of lizards (Bennett, 1982), and that aerobic metabolic scope of reptiles is slightly less than that of mammals (Hammond & Diamond, 1997). Hence, the maximum range of open capillaries in reptiles was estimated to be 20–500 $\mathrm{mm^{-2}}$. By analogy with the increase of perfused capillaries with increasing metabolic rate, it was assumed that the number of open capillaries increased proportionally to heart rate. The latter assumption is supported by experimental findings showing that subdermal blood flow and heart rate both increase as a result of heating the surface of lizards (Morgareidge & White, 1972) and a crocodile (Grigg & Alchin, 1976). Also, these estimates of capillary density agree broadly with values determined for frog skin, which range from six (Malvin, 1993) to 400 perfused capillaries $\mathrm{mm^{-2}}$ (Krogh, 1919).

Convective heat transfer by blood flow was calculated assuming that the thermal behaviour of blood flow can be expressed as internal flow through a circular cylinder with constant surface temperature (see below) (Incropera & DeWitt, 1996). Under these conditions, it can be assumed that the flow through the peripheral blood vessels is fully developed, i.e. the radial velocity component $v = 0$, and the gradient of flow velocity in the axial direction $\partial u/\partial x = 0$. Similarly, the flow is thermally fully developed when the temperature gradient of the fluid within the tube, referenced to the surface-bulk temperature difference, remains constant in the axial direction:

$$\partial[(T_s - T)/(T_s - T_m)]/\partial x = 0, \tag{9}$$

where T_s is the surface temperature and T_m the mean fluid temperature. In the case of constant surface temperature, $\mathrm{d}T_s/\mathrm{d}x = 0$, change in the mean fluid temperature is equal to the change in the axial direction in the difference between T_m and T_s:

$$\begin{aligned} \mathrm{d}T_m/\mathrm{d}x &= \mathrm{d}(T_s - T_m)/\mathrm{d}x \\ &= 2\pi r/mch\,(T_s - T_m), \end{aligned} \tag{10}$$

where r is the radius (m), m the mass flow ($\mathrm{kg\,m^{-3}}$), c the specific heat ($\mathrm{J\,kg^{-1}\,K^{-1}}$), and h the convection coefficient ($\mathrm{W\,m^{-2}\,K^{-1}}$). Integrating over the length of the tube (L) gives

$$(T_s - T_{out})/(T_s - T_{in}) = \exp(-2\pi r L/mch) \tag{11}$$

and the outflow temperature is

$$T_{out} = T_s - \{[\exp - (V/mch)]\,(T_s - T_{in})\}, \tag{12}$$

where V is the volume of the blood vessel. The heat transfer rate is then

$$q = mc\,[(T_s - T_{in}) - (T_s - T_{out})] \tag{13}$$

and, substituting for mc,

$$q = hA\{[(T_s - T_{out}) - (T_s - T_{in})]/\ln[(T_s - T_{out})/(T_s - T_{in})]\}, \quad (14)$$

where A is the cross-sectional area of the tube. The convection coefficient can be calculated from the definition of the Nusselt number (Nu),

$$h = Nuk/2r, \quad (15)$$

where $Nu = 3.66$ for radial flow with constant surface temperature (Incropera & DeWitt, 1996), and k is the conductivity ($\mathrm{W\,m^{-1}\,K^{-1}}$).

The convection analysis necessitates the assumption that $\mathrm{d}T_s/\mathrm{d}x = 0$ for each blood vessel; however, it may be unrealistic to assume that $T_s = T_e$, the operative environmental temperature of the lizard external skin surface, for all blood vessels. Therefore, T_s was estimated for each plane in the three-dimensional microvascular network by firstly determining the total heat conducted between the core and the surface of the animal (q_{cd}), and then calculating

$$T_s = q_{cd}L_j/r + T_e, \quad (16)$$

where L_j is the distance between plane j and the surface of the animal.

The total heat transfer by blood flow was calculated by adding heat transfer rates calculated for each perfused segment per mm^2 of the microvascular network and then multiplying by lizard surface area. Lizards were assumed to have a uniform initial body temperature $T_b = T_i$ before moving into a thermally different environment with temperature $T_c \neq T_b$. Heat is then conducted between the surface and the core, and convected by blood flowing from the core through the arterial network to the surface capillaries and via the venous network back to the core. The initial inflow temperature $T_{in} = T_i$ at time $t = 0$, and the outflow temperature of a segment of order j becomes the inflow temperature of a segment of the next order, $T_{out\,j} = T_{in\,j\pm 1}$. Inflow temperature at the first arterial segment at $t = i$ is equal to T_b at $t = i - 1$, $T_{in\,t=i} = T_{b\,t=i-1}$ where $T_{b\,t=i-1}$ is determined by both conduction and convection over the time interval i, which is arbitrary.

In the calculations predicting field data, I used the median of the T_e determined during heating and cooling episodes in the field (Seebacher, 1999). Similarly, when comparing calculated and measured rates of T_b change, I used the median heart rate measured during a heating or cooling episode in the calculations. A heating or cooling "episode" refers to an occasion when an animal moved into a microenvironment where $T_e \neq T_b$ and remained stationary in that environment long enough for T_b to change, approaching T_e. Typical examples are, for heating, exposure to full sun in the morning after emerging from a nocturnal shelter site or, for cooling, retreating into the shade after sun exposure.

Rate of T_b change was expressed as the rate of change of the dimensionless temperature $-\mathrm{d}\theta/\mathrm{d}t$ [recall that $\theta = (T_b - T_e)/(T_i - T_e)$]. In other words, the change of θ with time signifies the decrease of the difference between T_b and T_e with time as a proportion of the total, initial temperature step. The thermal time constant, which has often been used to describe changes in temperature (Smith, 1976) is the inverse of $-\mathrm{d}\theta/\mathrm{d}t$ (Turner & Tracy, 1985).

3. Results

It was possible to predict T_b accurately for heating and cooling in both species of lizard using the theoretical analysis of heat transfer via conduction and blood flow (Fig. 2). Heat transfer by conduction alone (shown separately in Fig. 2) underestimated the measured rate of T_b change, but including heat transferred by blood flow to the total heat exchange gave a good estimate of measured T_b change for heating and cooling in both species (Fig. 2). In order to test the applicability of the theory to real-life situations, all measured heating and cooling data were theoretically predicted for each individual of both *Pogona* (total $n = 106$ episodes) and *Varanus* (total $n = 67$ episodes) using measured heart rate and environmental conditions in the field. There were no significant differences between predicted and measured values for any of the lizards (Mann–Whitney test, all $p > 0.15$), and the combined data for each species are shown in Fig. 3.

The relative contribution of convection by blood flow to total heat exchange is likely to be

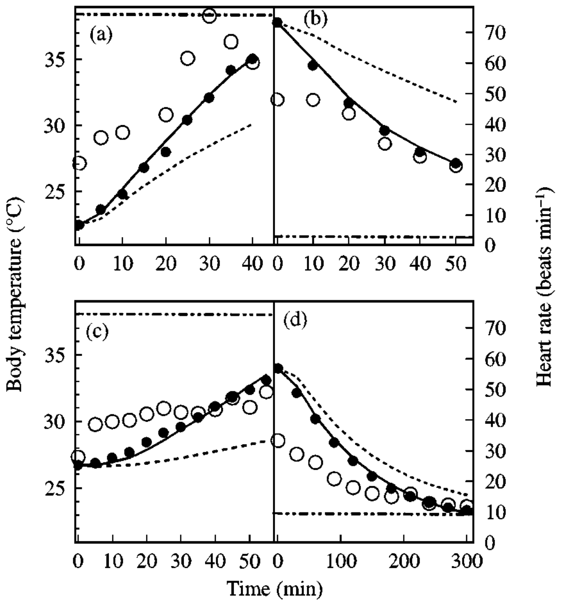

FIG. 2. Representative examples of measured and predicted rates of heating and cooling in *Pogona* and *Varanus*. Measured heart rate (○) and measured T_b (●) are shown as well as calculated T_b change owing to conduction alone (- - - -), and predicted T_b including heat transfer by conduction and blood flow (——); (a) and (b) *Pogona*, (c) and (d) *Varanus*. Median T_e for each heating and cooling episode is also shown (–- - -).

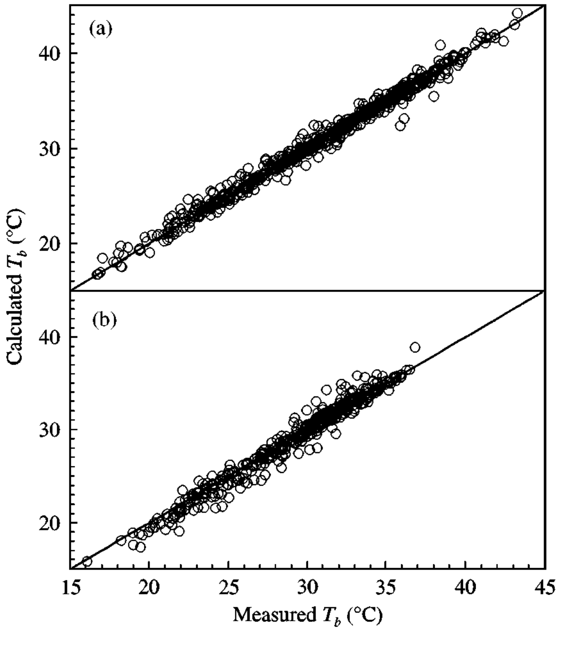

FIG. 3. Calculated T_b plotted against measured T_b for *Pogona* (a) and *Varanus* (b). There were no significant differences between calculated and measured T_b, and the lines of equality are shown.

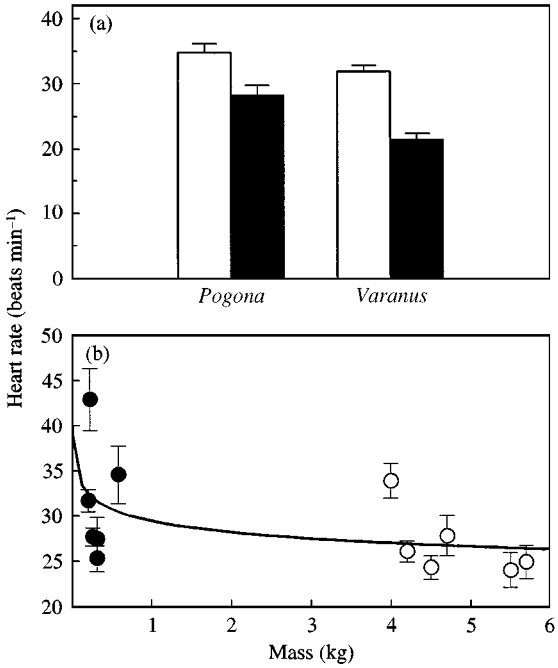

FIG. 4. Heart rate was significantly faster during heating than during cooling in both *Pogona* and *Varanus* (a), [(□) heating, (■) cooling], and heart rate decreased significantly with mass (b) [(●) *Pogona*, (○) *Varanus*]. Heart rates shown were standardized for 25°C.

modified physiologically by heart rate. In resting animals in the field, heart rate decreased significantly with mass ($F_{11,358} = 9.61$, $p < 0.0001$), and it was significantly slower in *Varanus* compared to *Pogona* ($F_{1,358} = 24.79$, $p < 0.00001$). Furthermore, heart rate during cooling was significantly slower than during heating ($F_{1,358} = 69.66$, $p < 0.00001$) (Fig. 4).

The rate of measured T_b change increased with increasing heart rate (Fig. 5). From theory, heat transfer by conduction is independent of heart rate, so that the change in θ with heart rate can be fully explained by the increase in the rate of convective heat transfer (Fig. 5). At low heart rate (up to 15–20 beats min^{-1}), measured T_b change is similar to that predicted to occur by conduction alone. As heart rate increases, however, measured T_b follows the curve predicted by the heat transfer rate owing to conduction plus blood flow. Up to a heart rate of 50–60 beats min^{-1}, θ increases quadratically owing to the increase of perfused capillary density over the body surface area. At higher heart rates, however, the increase in θ slows because heat exchange is limited by the

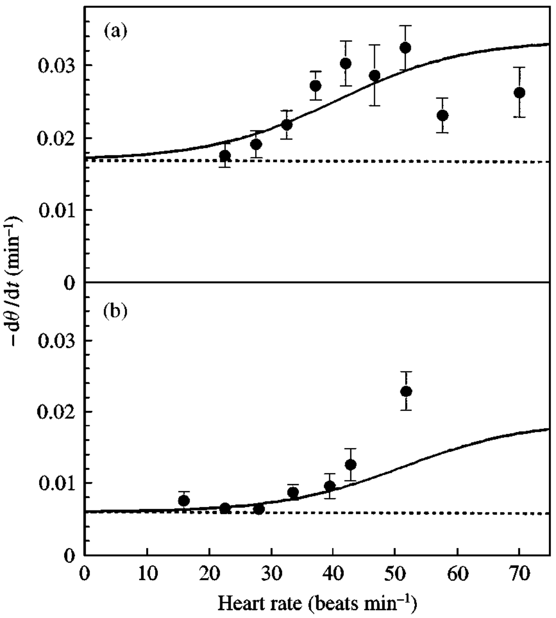

FIG. 5. Change in dimensionless temperature [$\theta = (T_b - T_e)/(T_i - T_e)$] as a function of heart rate. Temperature change due to conduction alone was independent of heart rate (----), but the contribution of blood flow to total heat transfer increased with heart rate in both species [solid line: (a) *Pogona*, (b) *Varanus*]. Theoretical predictions including both conduction and blood flow (——) predicted measured data (●) very well except at high heart rates.

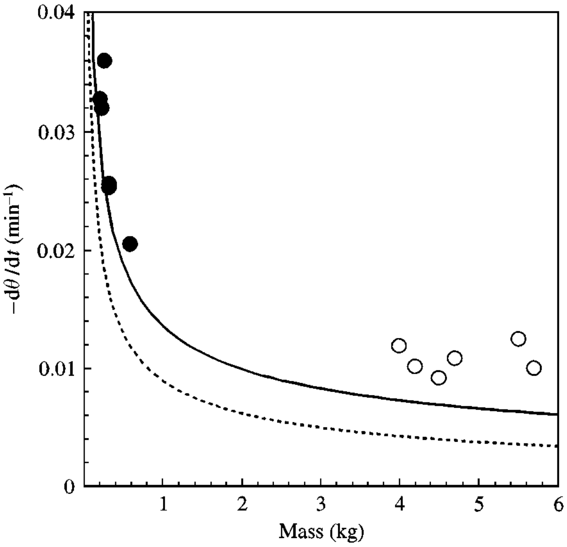

FIG. 6. Rate of change of dimensionless temperature decreased with body mass [measured field data: (●) *Pogona*; (○) *Varanus*], but heat transfer by conduction (----) scaled differently with mass ($Y = 0.00903\text{Mass}^{-0.54}$) than heat transfer by blood flow (——; $Y = 0.00469\text{Mass}^{-0.31}$).

more rapid decrease in the difference between T_b and T_e. Interestingly, measured data depart from the predicted curves at high heart rates (> 55 beats min^{-1}), but the change in θ is less than that predicted in *Pogona*, and greater than that predicted in *Varanus*. Note, however, that heart rates of 50 beats min^{-1} or higher were observed in only 5% of all heating or cooling episodes in *Varanus*, and in 10% of those in *Pogona*.

The change in measured θ decreased with mass and, again, this change was predictable from theory. Heat transfer by both conduction and convection via blood flow decreased with mass, explaining the observed relationship in the measured data, except that data for *Varanus* fell somewhat above the predicted line (Fig. 6). An important point to note is that heat transfer by blood flow scaled with mass to the power of -0.31, as expected because heat is transferred from the surface to contribute to temperature change of the lizard volume, but heat transfer by conduction scaled with mass to the power of -0.54. Conduction scales with increasing radius which implies a dependency on the surface to volume ratio. However, it also scales with the external boundary layer which increases with the length of the animal and causes the convection coefficient to decrease, thereby decreasing the Biot number and explaining the lower scaling exponent than would have been expected from the surface to volume ratio. This difference in the scaling exponents has implications for the relative contributions of conduction and blood flow to the total heat transfer as mass increases (Fig. 7). As expected from Fig. 5, the relative contribution of blood flow to total heat transfer increases with heart rate [Fig. 7(a)]. More surprisingly and, as mentioned above, as a result of the different scaling exponents, the relative importance of blood flow also increases with body mass [Fig. 7(b)].

4. Discussion

Bartholomew & Tucker (1963) reported for the first time that live *Pogona* (then *Amphibolurus*) heated and cooled faster than dead ones, that live lizards heated faster than they cooled and that heating and cooling rates were correlated with

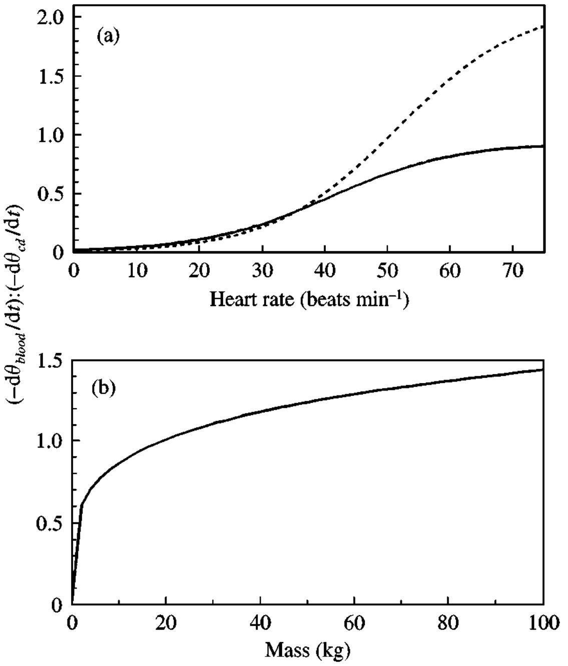

FIG. 7. The relative importance of conduction and blood flow in total heat transfer as a function of heart rate (a) [(----) *Varanus*; (——) *Pogona*] and body mass (b). For values < 1 heat transfer by conduction is greater than by blood flow, while for values > 1 heat transfer rate by blood flow exceeds heat transfer by conduction. Remember, however, that absolute rates of T_b change decrease with mass (see Fig. 5).

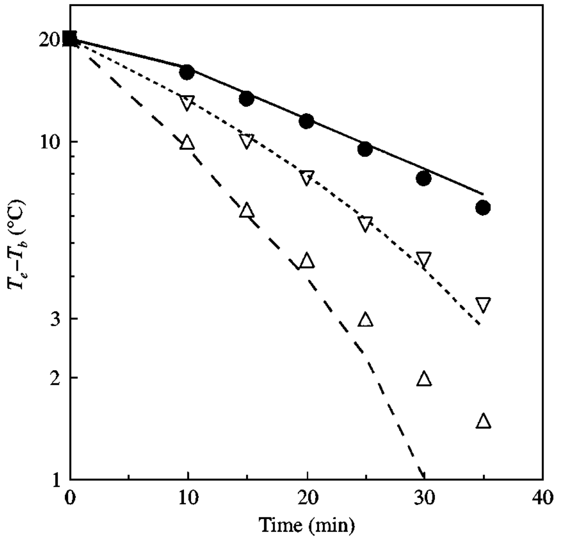

FIG. 8. Theory predicted the original data of Bartholomew & Tucker (1963) on heating and cooling on *Pogona* very well, indication that changes in heart rate and blood flow explain the differences observed between live and dead animals, and between heating and cooling [measured data for dead lizard (●) (Bartholomew & Tucker, 1963), predicted data for dead lizard (——); measured data for cooling, live lizard (▽) predicted data for cooling, live lizard (----); measured data for heating, live lizard (△) predicted data for heating, live lizard (– – –)]. The Bartholomew and Tucker (1963) experiment involved heating and cooling a *Pogona* in air by transferring it from a 20°C environment to 40°C for heating, and vice versa for cooling. To facilitate comparisons, the graphic presentation of this figure is identical to that in Bartholomew and Tucker (1963; Fig. 3).

changes in heart rate which was significantly faster during heating than during cooling. I applied my theoretical analysis to the Bartholomew & Tucker (1963) original T_b data (their Fig. 3) to see if theory can account for the patterns observed (Fig. 8). Choosing heart rates typical for *Pogona* observed by Bartholomew & Tucker (1963) and in the present study (median 45 beats min^{-1} during heating and 25 beats min^{-1} during cooling) I was able to predict the Bartholomew and Tucker data very accurately except for overestimating the rate of heating somewhat. Dead animals heat and cool by conduction alone (Fig. 8), while the difference between rates of heating and cooling in live lizards is fully explained by the differences in heart rate and the resultant different rates of convection by blood flow.

The departure of the field data from the theory predicting heat transfer by blood flow at high heart rates (Fig. 5) may be explained by the different physiologies and lifestyles of *Pogona* and *Varanus*. Varanid lizards are the most active lizards and have the highest aerobic metabolic rates among the reptilia (Bartholomew & Tucker, 1964; Thompson & Withers, 1997), while *Pogona* is a more "typical", sedentary reptile (Bennett, 1982; Grigg & Seebacher, 1999). If capillary density scales with metabolic rate in reptiles as it does in mammals, it may be that the maximum number of capillaries per unit area is greater in *Varanus*, but less in *Pogona* than I estimated. The relationship between metabolic rate and cardiovascular structure in reptiles needs to be determined experimentally to confirm or improve my estimates. In this context, it should be considered also that perfusion of the body volume is possible by pulsating flow only as resistance to mass transfer would be too great otherwise (Bejan, 1997a). Hence, the structure of the cardiovascular system may, to a certain extent, determine heart rate and metabolic rate.

An interesting technical point to note is that an increase in the diameter of blood vessels, commonly referred to as vasodilation, does not increase the rate of heat transfer, because it increases the mass flow which decreases the rate of heat transfer (see Section 2 above). However, an increase in the number of small vessels of constant small diameter, such as capillaries, will increase the rate of heat transfer, and it is likely that the increase in the number of perfused capillaries per unit area is accompanied by vasodilation of larger supply vessels to increase the blood flow rate. Note that the constant diameter of the smallest duct size in the microvascular network (capillaries) is predicted from constructual theory (Bejan, 1997b) and, subsequently, this feature formed one of the initial assumptions in the fractal analysis of cardiovascular systems (West *et al.*, 1997).

Apart from different rates of heating and cooling, and differences between live and dead animals, much of the focus of previous research has been on the effect of mass on rates of heating and cooling (Smith, 1976; Grigg *et al.*, 1979; Turner & Tracy, 1985a, b). In particular, it has been shown that the ratio of rates of heating to rates of cooling increases (i.e. the ratio of time constant during heating to time constant during cooling decreases) with increasing mass (Smith, 1976; Grigg *et al.*, 1979), but the reasons for this observation have remained unclear up to now. I have provided an explanation by demonstrating that the relative importance of heat transfer by blood flow increases with increasing mass because of the different scaling exponents for heat transfer by conduction and convection by blood flow [Fig. 6(b)]. Mass scaling relationships in biology are often complex, and do not behave according to a single allometric power law (Feldman, 1995). The present study is an example where a biological function, heating and cooling, has to be broken up into its components to reveal its true scaling relationship. It is important to remember, however, that the effect of changes in heart rate on heat transfer is superimposed on the mass relationship, and this may explain some anomalous results obtained by previous workers (Grigg & Alchin, 1976).

Grigg *et al.* (1979) presented regression lines which predicted that small lizards should heat slower than they cool. There is no physical, mass-related explanation for this, but the results could have been obtained if the experimental animals had higher heart rates during cooling than during heating. Alternatively, Fraser & Grigg (1984) propose a number of factors, such as water loss and evaporative cooling, which may have produced these results and they concluded that the observation is unlikely to represent an adaptive response. Moreover, Turner & Tracy (1985a) have cast some doubt on the validity of data (from Smith, 1976) used by Grigg *et al.* (1979) to derive their regression equations. As an alternative, Turner & Tracy (1985a) proposed that the ratio of heating : cooling rates in American alligators increases with body mass up to around 5 kg when it decreases as body mass continues to increase, but an explanation for this rather unusual pattern remains elusive. It may be that the susceptibility of crocodilians to stress and the bradycardia associated with it, as well as the unique cardiovascular system of crocodilians (Axelson & Franklin, 1997) partly explains these results. Also, Turner & Tracy (1985a) made use of the same data set they suggested may be invalid with reference to the work of Grigg *et al.* (1979).

The present work is not the first attempt to develop a theoretical model detailing heat transfer by blood flow in ectotherms. It is, however, the first to calculate heat transfer within a realistic microvascular network. Other authors have incorporated blood flow in heat transfer models by simply changing the conductivity of tissue, or conductance through the body wall (Grigg *et al.*, 1979; Dunham *et al.*, 1989; O'Connor, 1999). This is inappropriate in the sense that the parameters determining convective heat transfer by blood flow, such as convection coefficients, flow rates and pressures, are substituted by an *ad hoc* conduction term which is unrelated to convective heat transfer by blood flow (Robertson & Smith, 1981). Furthermore, few previous studies have made an attempt to validate model predictions against empirical field data, making them highly speculative, especially considering the number of simplifying assumptions which have to be made commonly in biophysical analyses (O'Connor & Spotila, 1992).

Changes in heart rate in response to heating and cooling have been interpreted to be of functional significance because they enable reptiles to heat faster in the morning and cool slower in the evening so that the net gain is an increase in the time the animal can be active at a high T_b (Bartholomew, 1982; Turner & Tracy, 1985b; Grigg & Seebacher, 1999). With my theoretical model, I am, for the first time, able to quantify the potential benefit of heart rate "hysteresis" during heating and cooling. For example, on a typical day, *Pogona* basks in the morning [Fig. 9(a), basking indicated by the filled rectangle above the x-axis] thereby raising T_b to the preferred T_b range (Grigg & Seebacher, 1999). T_b remains high during the day, until the environment cools and the lizard retreats into vegetation [Fig. 9(b) hatched rectangle above the x-axis]. I predicted T_b during the heating phase in the morning and the cooling phase in the evening [both periods indicated by the rectangles in Fig. 9(a)] firstly using heart rate measured in the field [Fig. 9(a), median measured heart rate 43 beats min^{-1} during heating and 22 beats min^{-1} during cooling], and then, to quantify the effect of heart rate hysteresis, I predicted T_b with heart rate 10 or 20 beats min^{-1} slower during heating or faster during cooling [Fig. 9(b) and (c)]. A decrease of 10 beats min^{-1} during basking meant that the lizards had to bask 8 min longer to reach the T_b observed in the field at the end of the basking episode, and if heart rate was reduced by 20 beats min^{-1}, which is similar to heart rate observed during cooling, basking time would be increased by 22 min. Similarly, the lizard would cool much faster at higher heart rates, and it would cool to the same T_b as observed in the field 36 or 47 min faster if heart rate was increased by 10 or 20 beats min^{-1}, respectively. Hence, the benefit of heart rate hysteresis is quite considerable, and, reversing the measured heart rate pattern for heating and cooling, i.e. heart rate 20 beats min^{-1} slower during heating and 20 beats min^{-1} faster during cooling, would shorten the time the lizard in this example could spend with T_b at preferred levels during the day by 69 min. If heart rate during heating was the same as during cooling, for example near 30 beat min^{-1} ($\pm$ 10 beats min^{-1} in Fig. 9(b) and (c)], the time that could be spent within the preferred T_b in a day would be reduced by 44 min.

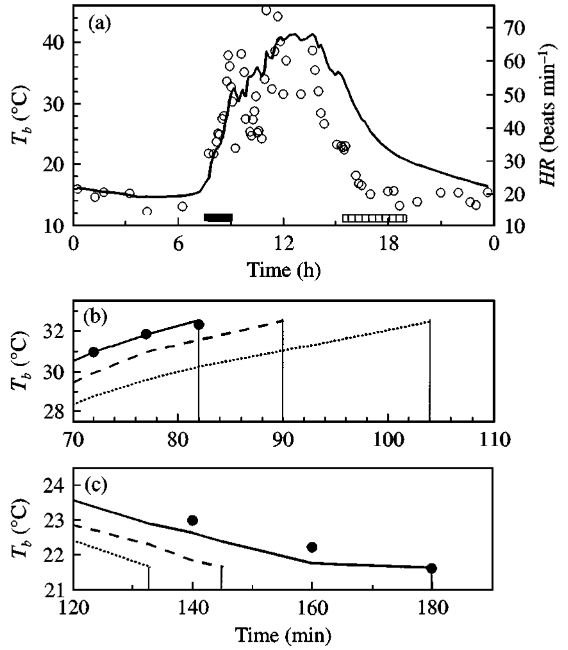

FIG. 9. The functional significance of heart rate hysteresis between heating and cooling demonstrated on a typical example of a diurnal T_b [——, (a)] and heart rate [○, (a)] record from *Pogona* (a). The morning basking phase [period indicated by the solid bar above the x-axis in (a)] was predicted for measured heart rate values [——, (b)] and for heart rate values which were 10 beats min^{-1} [- - - -, (b)] and 20 beats min^{-1} [· · · ·, (b)] slower than measured values. Similarly, the afternoon cooling phase (hatched bar above the x-axis in (a)] was predicted for measured heart rate values [——, (c)] and for values exceeding measured heart rate by 10 beats min^{-1} [- - - -, (c)] and by 20 beats min^{-1} (· · · ·, (c)]. Note that only the final parts of the heating and cooling episodes are shown in (b) and (c).

Hence, given the thermal sensitivity of physiological rate functions (Hazel & Prosser, 1974), changes in heart rate during the heating and cooling are likely to be of adaptive significance. An extra 44 min per day during which T_b is within the preferred range, and performance is at an optimum, is likely to confer a selective advantage on an animal, such as *Pogona* or *Varanus*, showing heart rate "hysteresis" compared to one which does not. However, heart rate hysteresis is unlikely to be of ecological significance for very large reptiles, because overall heating and cooling rates in very large animals, such as large crocodiles (> 30 kg; Grigg *et al.*, 1998) or dinosaurs (Seebacher *et al.*, 1999), would be so low and animals would respond to cyclic diurnal and seasonal changes in environmental temperatures rather than to acute changes brought about by a change in posture (see e.g. Grigg *et al*., 1998; Seebacher, 1999). Therefore, changes in heat transfer by blood flow would be unimportant, because they could not change the mean around which diurnal T_b oscillates in very large ectotherms (Seebacher *et al*., 1999). Nonetheless, there may be an evolutionary significance of heart rate "hysteresis" in large ectotherms as it may bestow advantages on juveniles.

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