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Thermographic Analysis of Body Surface Temperature of Mammals

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Among mammals, the similarity in body temperature indicates that body size differences in heat loss must match the body size differences in heat production. This study tested the possibility that body surface temperature (Tbs), responsible for heat loss through radiation and convection, may vary systematically with the animal's body mass (M). Tbs was measured by whole body thermography in 53 specimens from 37 eutherian mammals ranging in M from a few grams to several tons. Numerous thermographs were taken from all angles, indoor, with the animals standing still in absence of air convection and of external radiant sources, at the ambient temperature of 20–22°C, 22–25°C, or 25–27°C. Data were analysed as whole body surface average, as average of the "effective" body surface area (those regions with temperatures exceeding ambient temperature by > 1.5°C or by > 5°C), as the peak histogram distribution and as average of the regions with the top 20% temperature values. For all modes of data analysis and at all ambient temperatures Tbs was independent of the animal's M. From these data, the heat loss by radiation and natural convection combined was estimated to vary to the 2/3 power of M. It is concluded that, for the same ambient conditions, the surface temperature responsible for radiation and convection is essentially body-size independent among mammals.

Key words: body surface, heat loss, skin temperature, thermoregulation

INTRODUCTION

At rest, body temperature (Tb) can differ by a few degrees among eutherian mammals (Mortola and Lanthier, 2004), but body size does not appear to influence it in a consistent manner (Piccione et al., 2005; Mortola and Maskrey, 2011). Differently, heat production per unit of body mass (M) is neither similar among species nor directly proportional to M. In fact, since its early measurements (Kleiber, 1932), heat production has been shown to scale to the 0.75 power of M (Peters, 1983; Schmidt-Nielsen, 1984). The physiological basis for such scaling patterns continues to be the subject of various interpretations (Dodds et al., 2001; Gillooly et al., 2001; West et al., 2002; Glazier, 2005). Body temperature results from the balance of heat production and heat loss; the lack of correlation between Tb and M among mammals should thus imply that heat loss scales to M approximately as heat production does, or $M^{0.75}$.

Many variables are involved in heat loss, and most of them may have some scaling pattern with M. Heat transfer by conduction to the ground may be larger in very small animals with short legs. Cutaneous and pulmonary evaporation could play a relatively greater importance in smaller species, which have larger body surface area (in relation to M) and higher M-specific pulmonary ventilation (Stahl, 1967). In the standing posture under ordinary ambient conditions when skin temperature exceeds ambient temperature, the major mechanisms of heat dispersion are air convection and radiation, which depend on the body surface area exposed to the environment and the body-ambient temperature gradient. The former is undoubtedly smaller (relative to M) in larger species, although the portion of it effectively engaged in heat transfer, or effective surface area (ESA), can vary according to morphological and functional factors. With respect to the temperature gradient, measurements with thermocouples from three cutaneous regions in five mammals of largely different sizes, indicated that skin temperature increased with the animal's M (Piccione et al., 2005), suggesting that, in addition to body surface, the temperature gradient is also involved in the scaling pattern of heat loss.

However, the physiological value of data obtained by skin thermocouples is limited by the arbitrariness in the choice of the skin regions sampled, usually hairless or shaved areas. In fact, what matters for body radiation is not the skin temperature per se, but the temperature of the outer layer surrounding the animal, or body surface temperature (Tbs), which must include any hairy, furred, or woolly areas. The question asked in this study refers to this latter variable; specifically, whether or not Tbs, when measured under identical ambient conditions, varies systematically among mammals of different body size. Infrared thermography offers a unique opportunity to evaluate the Tbs that effectively contributes to body radiation in undisturbed conditions. Previously, Phillips and Heath (1995) used thermographic measurements of 29 mammalian species to estimate the

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changes in ESA between warm and cold conditions. Their aim did not necessitate the measurements to be collected under identical ambient conditions (in fact, some data were collected outdoor), and no data of Tbs were provided. Therefore, interspecies comparative data of Tbs under constant ambient conditions are unavailable. The current study, through the analysis of multiple thermographs from specimens of 37 mammalian species spanning a 10^5 range in size, while standing in indoor enclosures at the same ambient temperature in absence of forced air convection, examined whether Tbs varies systematically with body size.

METHODS

Measurements of body surface temperature (Tbs) were obtained on 53 specimens from 37 eutherian species, varying in body mass (M) from 0.02 and 4,300 kg. Two were laboratory species (mouse and rat); all others were domesticated or wild species maintained in captivity. Monotremata, marsupials and chiroptera were excluded because of their propensity for low metabolic rate and Tb. All animals were studied indoors, shielded from sunlight or other sources of radiant heat, in still air conditions, with minimal artificial light. Most often (86% of cases) measurements were collected during morning hours in the same quarter where the animal had spent the night. The animals were in quiet wakefulness, standing still, with no restraints or handling. Data from specimens seated or lying down, or from periods immediately following activity, were excluded. The female animals were not lactating, pregnant, or in oestrus. Ambient temperature and relative humidity were monitored by a data logger (Hobo H8, Onset Corp., Bourne, MA; 0.5°C resolution) placed at about the height of the animal. The accuracy of the data logger was checked against a bulb-thermometer. Measurements were collected at one of three ambient temperatures, 20–22°C (*n* = 17), 22–25°C (*n* = 24), and 25–27°C (*n* =12). Body mass (M, in kg) was either measured or, when weighing would have caused distress to the animal or was unpractical, was derived from standard bibliographic references for gender and age (e.g., Silva and Downing, 1995). From M, body surface area (SA) was computed according to the formula SA (m^2) = 0.1 · M $(kg)^{2/3}$ (Peters, 1983). If both enclosures and animals were assumed to be spheres, for each specimen studied the ratio of the radius between the two spheres usually ranged between 4 and 8. This means that the emissivity of the white walls of the enclosures played a negligible effect on the emittance factor $F\varepsilon$ (Blaxter, 1989), which is one factor in the estimate of the net infrared radiation exchange (Appendix).

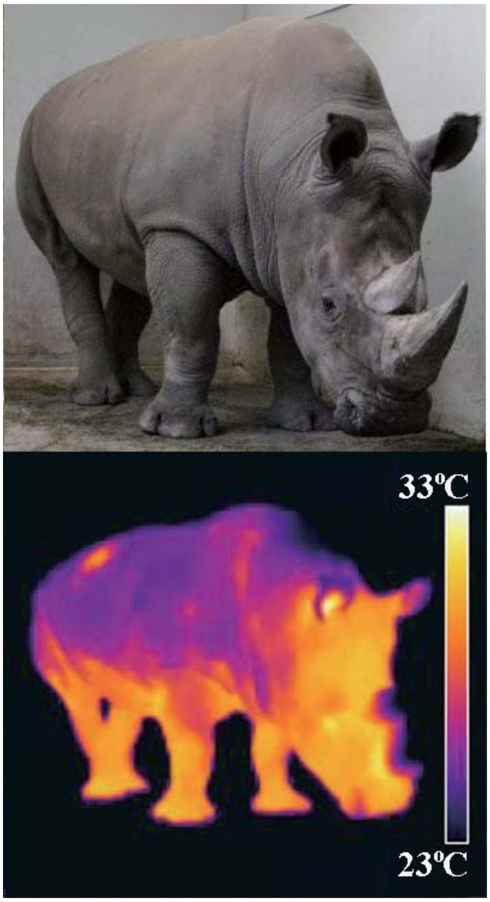

Fig. 1. An example of thermograph in a rhinoceros, taken at the ambient temperature of 20.9°C. For comparison purposes the corresponding standard digital picture is presented at top.

Thermographs were taken with a high-sensitivity infrared camera (Flir Systems Inc, i7 model, $144 \cdot 10^2$ pixels, < 0.1°C thermal sensitivity) from a distance between 30 cm to 5 meters, depending on the size of the specimen. Out of a large number of images taken from different viewing angles, an average of eight thermographs per animal were selected for analysis, aiming to an equal representation of the back, front, right, and left sides, and the head region. After adjusting for distance, ambient temperature, and humidity, the thermograph was cropped down to the animal silhouette. Emissivity (ε) was considered constant at 0.95, although it is possible that in some animals the pelt had ε values slightly closer to 1 (Hammel, 1956). The possibility that systematic differences in ε could modify the conclusions has been taken into account (see Results).

The thermograph was exported to an Excel® spreadsheet for

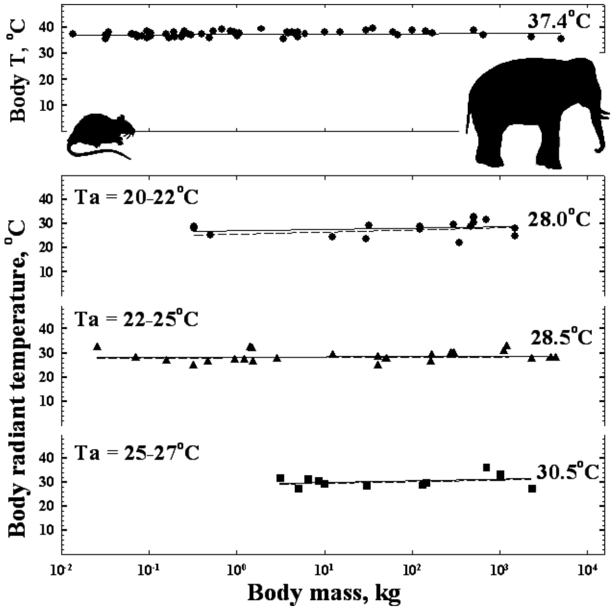

Fig. 2. Average body surface temperature as function of body mass for the three sets of animals studied at the ambient temperature (Ta) indicated. Data of body temperature (panel at top), from various bibliographic sources (e.g., Mortola and Lanthier, 2004; ISIS, 2002), are presented for purposes of comparison. Each symbol is a different animal. Continuous lines refer to the best-fit linear regressions through the data points; none of them differed significantly from zero. The dashed lines (barely visible below the continuous lines) are the linear regressions computed through data recalculated with emissivity = 1. Values at right are the means of body surface temperature of all specimens.

four forms of analysis. The first consisted simply in the computation of the average Tbs from the individual pixels of all body regions, irrespective of the type of hair coverage. The few exceptions were some specific ‘cold’ regions, such as the long white locks of hairs of the tail of the colobus (*Colobus guereza*) or the horn of the white rhinoceros (*Ceratotherium simum*) (Fig. 1). The inclusion of these appendages, which do not participate to heat transfer and have a temperature close to ambient, would have caused a small, yet unjustified, reduction in the average Tbs.

It has been suggested that a temperature gradient of less than 1.5°C is likely too small for meaningful heat exchange (Phillips and Heath, 1995). Hence, the second analysis consisted in the computation of the average Tbs of the effective surface area (ESA1.5), defined as the sum of all body surfaces with temperatures at least 1.5°C above ambient. The variability within ESA1.5 was computed from its coefficient of variation (CV = standard deviation/mean). The third analysis consisted in computing the Tbs of the highest peak of the histogram distribution of all pixels. This approach would yield the same numerical result as the overall average only if the values were normally distributed. However, this was often not the case. In fact, in some animals Tbs differed substantially from one region to the next (e.g., in the rhino of Fig. 1, back and sides by comparison to head and legs), introducing multiple peaks, or long tails, in the histogram distribution. Finally, Tbs was computed as the average of all pixels with the highest 20% values. This analysis may seem redundant to that of the average Tbs of the whole body; however, it addresses the possibility that heat transfer may increase disproportionately with increase in Tbs. In fact, between two surfaces with the same average temperature, the surface with the larger variability in temperature will transfer more heat, as heat transfer increases disproportionately with temperature.

Finally, to test whether the conclusions could have changed had the threshold of the ESA been different than 1.5°C, values of Tbs were recalculated for ESA5, that is, the cumulative body surface with at least 5°C above ambient temperature.

The statistical significance of a difference between sets of data (presented as means ± 1 SEM) and of the correlation coefficients of the linear regressions have been evaluated by two-tailed *t* test, with significance accepted at $P < 0.05$.

RESULTS

Figure 2 presents the average Tbs as function of the animal M for all the specimens studied (Table 1). For comparison purposes, the top panel of the figure presents the corresponding data of body temperature, derived from various compilations (e.g., Mortola and Lanthier, 2004; ISIS, 2002).

The slopes of the best-fit functions correlating Tbs to M were 0.00006 (at Ta = 20–22°C), 0.00002 (at Ta = 22–

Table 1. [1]When more than one specimen, reported value indicates the average. Missing values under the ESA5 column indicate that ESA5 was < 1% of the total body surface. M, body mass. Ta, ambient temperature. ESA1.5 and ESA5 refer to the effective surface area with temperatures, respectively, at least 1.5°C or at least 5°C above ambient temperature.

Order	Species	Specimens (gender)	M[1], Kg	Ta[1], °C	Body surface temperature[1], °C		
					Total	ESA1.5	ESA5
Artiodactyla	Bactrian Camel - *Camelus bactrianus*	1 (m)	474	21.5	28.7	28.7	29.2
	Bighorn Sheep - *Ovis canadensis*	1 (f)	41	24.5	27.6	28.0	–
	Cow - *Bos taurus*	2 (f)	700	23.8	33.8	33.8	34.0
	Eland, Common - *Taurotragus oryx*	3 (2m,f)	500	20.3	31.9	31.9	32.1
	Giraffe - *Giraffa camelopardalis*	1 (m)	1200	23	32.7	32.7	32.8
	Hippopotamus - *Hippopotamus amphibius*	1 (m)	2300	24.8	27.5	28.9	30.6
	Pig - *Sus scrofa*	1 (f)	295	22	29.7	30.1	–
	Sheep - *Ovis aries*	1 (f)	50	24.5	27.6	28.0	–
	Yack - *Bos grunniens*	1 (m)	350	20	21.8	27.8	29.2
Carnivora	Amur Leopard - *Panthera pardus orientalis*	1 (f)	40	24.9	28.4	28.4	30.0
	Coati, White-nosed - *Nasua narica*	1 (m)	5	25	27.2	28.5	–
	Dog - *Canis lupus familiaris*	3 (2m,f)	15	21.3	28.7	29	29.9
	Lion - *Panthera leo*	2 (m,f)	138	24.5	28.7	29.2	30.6
	Ocelot -*Leopardus pardalis*	1 (m)	10	26	29.4	29.7	31.1
	Siberian Tiger - *Panthera tigris altaica*	1 (m)	164	24.7	29.4	29.5	30.2
	Skunk, striped - *Mephitis mephitis*	1 (f)	3	24.6	27.6	27.7	30.6
	Snow Leopard - *Panthera uncia*	1 (f)	30	23	23.5	23.6	26.4
	Spectacled Bear - *Tremarctos ornatus*	1 (m)	161	23	26.3	26.7	27.9
Cingulata	Armadillo Three-banded, Southern - *Tolypeutes matacus*	1 (m)	1.5	23.5	31.8	31.8	31.8
Erinaceomorpha	Hedghog, Four-toed - *Atelerix albiventris*	1 (f)	0.3	23	24.8	25.6	–
Lagomorpha	Rabbit - *Oryctolagus cuniculus*	1 (m)	1.3	23.2	27.2	27.3	30.2
Perissodactyla	Horse - *Equus caballus*	3 (m)	1050	24.8	32.1	32.1	32.4
	Przewalski’s Horse - *Equus ferus przewalskii*	1 (m)	122	21	29.7	29.8	30.2
	Rhinoceros, White -*Ceratotherium simum*	1 (m)	1485	21	28.4	28.5	29.2
	Zebra, Burchell’s - *Equus burchelli*	2 (f,m)	289	23.5	29.9	30.1	30.6
Primates	Mandrill - *Mandrillus sphinx*	2 (m,f)	19	24.7	30	30.1	31.2
	Patas Monkey - *Erythrocebus patas*	1 (f)	6.5	26.5	31.4	31.4	32.6
	Pigmy Slow Loris - *Nycticebus pygmaeus*	1 (f)	1.0	20	25.2	25.2	26.1
Proboscidea	Elephant, African - *Loxodonta africana*	2 (f)	4025	24	27.8	28	29.2
Rodentia	Agouti Golden (St Vincent) -*Dasyprocta leporina aguti*	1 (m)	3.1	25.3	31.6	31.6	32.4
	Chinchilla, Long-tailed - *Chinchilla lanigera*	1 (f)	0.46	22.8	26.3	26.3	28.6
	Golden Hamster - *Mesocricetus auratus*	1 (f)	0.16	23.7	26.9	27.2	29.4
	Mongolian Gerbil - *Meriones unguiculatus*	1 (unknown)	0.07	23.7	28.1	28.3	29.5
	Guinea Pig - *Cavia porcellus*	1 (unknown)	0.95	23.7	27.3	27.7	30.1
	Mouse - *Mus musculus*	1 (m)	0.025	24.9	32.2	32.2	32.3
	Porcupine, South African -*Hystrix africaeaustralis*	1 (f)	12.3	23.5	29.1	29.1	30.2

25°C), and 0.0002 (at Ta = 25–27°C); none differed significantly from zero. In fact, the Tbs intercept of these correlations closely corresponded to the average Tbs of each set of data, which increased from 28.0 ± 0.8°C at Ta = 20–22°C to 30.5 ± 0.7°C at Ta = 25–27°C ($P < 0.005$). Because a change in emissivity ε from 0.95 to 1 would lower Tbs by ~0.05°C for each degree increase in Tbs, the data were reanalysed assuming $\varepsilon = 1$. As expected, the individual data were displaced below the values obtained with $\varepsilon = 0.95$, by a magnitude that varied according to the animal's average Tbs; however, the slopes of the lines remained not significantly different from zero (dashed lines in Fig. 2).

The Tbs of ESA1.5 averaged slightly higher than that of the whole body surface, given that ESA1.5 eliminated the pixels with less than 1.5°C difference from ambient. The slopes of the M-Tbs (ESA1.5) relationships were 0.0004 (at Ta = 20–22°C), –0.00001 (at Ta = 22–25°C) and 0.0006 (at Ta = 25–27°C); none differed significantly from zero. When Tbs was computed from the peak of the histogram distribution, the slopes of the M-Tbs relationships were 0.0033 (at Ta = 20–22°C), 0.0003 (at Ta = 22–25°C) and 0.0008 (at Ta = 25–27°C). The numerical values of these slopes were consistently higher than those computed from the pixels of the whole body surface or from those of ESA1.5; however, under statistical analysis, none of the slopes differed significantly from zero. The variability of Tbs within ESA1.5, evaluated by its coefficient of variation (CV), could differ greatly among species; however, it changed systematically neither with body size (Fig. 3, left panels) nor with the ESA1.5 average temperature (Fig. 3, right panels).

The Tbs values of ESA5 were all higher than those of ESA1.5, as expected. However, the slopes of the M-Tbs (ESA5) relationships remained not significantly different from zero.

Analysis limited to the areas with the highest (top 20%) Tbs values did not reveal any systematic correlation with M (Fig. 4). Specifically, the slopes of the M-Tbs (top 20%) relationships were 0.0004 (at Ta = 20–22°C), –0.0008 (at Ta = 22–25°C) and –0.0013 (at Ta = 25–27°C); none differed significantly from zero.

The Tbs of the head examined in isolation exceeded the Tbs of the whole body (head included) in 78% of the cases, on average by 1.4°C (± 0.2) (Fig. 5).

ESA1.5 and ESA5 averaged, respectively, 92% (± 2) and 61% (± 5) of the total body surface area SA. The product between these percentages and SA (m^2) gave the cumulative area (m^2) of ESA1.5 and ESA5. The allometric (log-log) plots of these areas against the corresponding M produced

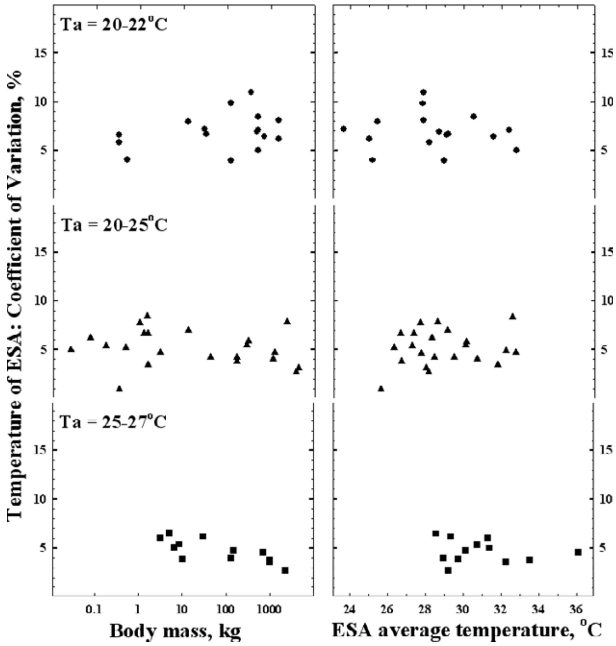

Fig. 3. Coefficient of variations (%) of the temperature of the effective surface area (with body surface temperatures at least 1.5°C higher than ambient, ESA1.5) as a function of the animal body mass (kg) (left panels) or of the average ESA1.5 temperature (°C) (panels at right), for the three sets of ambient temperatures (Ta).

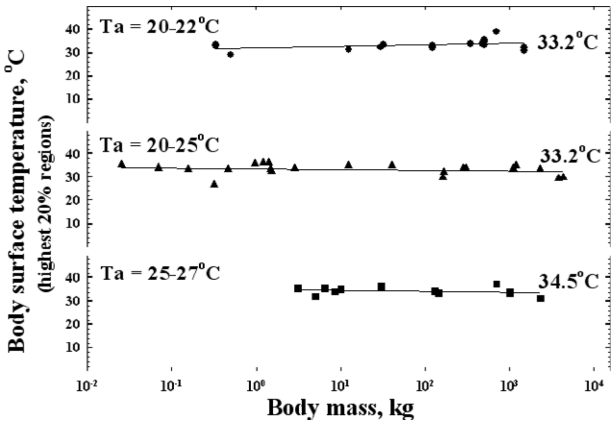

Fig. 4. Average body surface temperature (Tbs) of the regions with the highest 20% values, as function of the animal body mass (M), for the three sets of ambient temperatures (Ta). Each symbol is a different animal. Continuous lines refer to the best-fit linear regressions through the data points. The slopes of the M-Tbs relationships did not differ significantly from zero. Values on the right are the means of body surface temperature of all specimens.

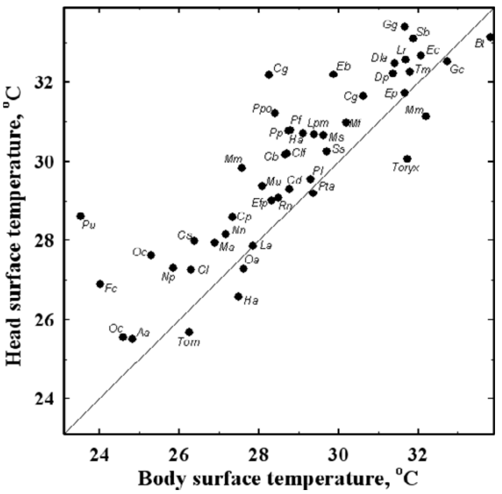

Fig. 5. Relationship between the radiant temperature of the head (Y-axis) and the average value of the whole body. The oblique line is the line of identity. Abbreviations refer to the initials of the species scientific names, as indicated in Table 1.

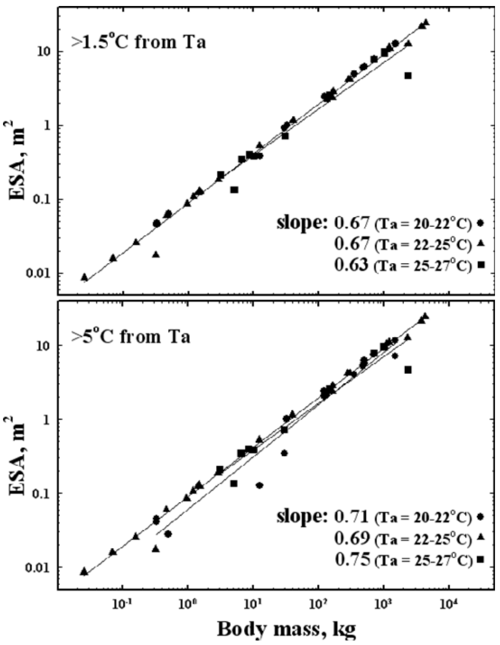

Fig. 6. Allometric (log-log) curves of the effective surface areas (m^2) with body surface temperatures at least 1.5°C higher than ambient (ESA1.5, top panel) or at least 5°C higher than ambient (ESA5, bottom panel), for each of the three ambient temperatures (Ta).

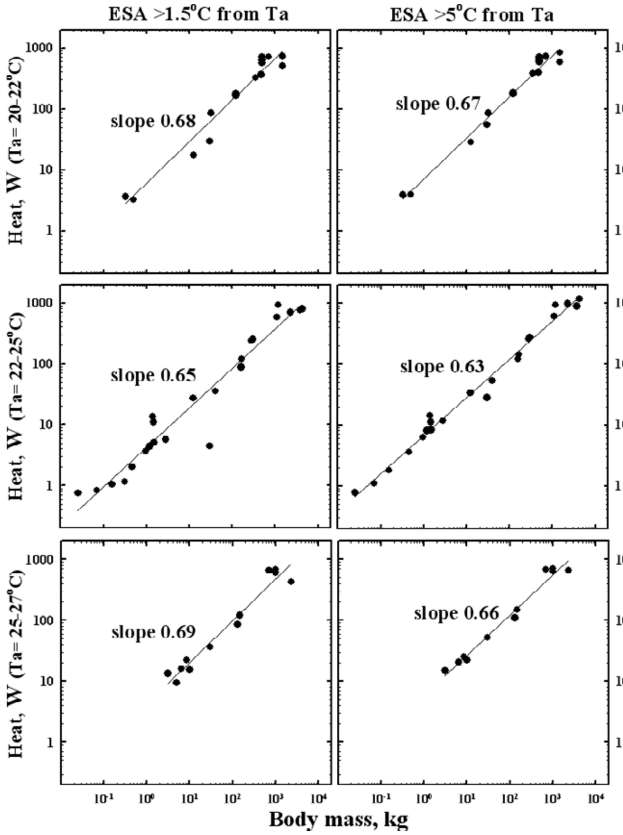

Fig. 7. Allometric (log-log) curves of the total heat loss (W) due to combined radiation and natural convection, from body surfaces with temperatures at least 1.5°C (ESA1.5, left panels) or 5°C (ESA5, right panel) higher than ambient, for each of the three ambient temperatures. The slopes of the regression lines are indicated.

slopes of ~0.66 and ~0.72 for ESA1.5 and ESA5, respectively (Fig. 6).

From the data of Tbs (°C) and SA (m^2) of ESA1.5 and ESA5, and under the assumption that each animal can be modeled by a sphere, it was possible to estimate total heat loss (W*total*) due to radiation (W*r*) and natural convection (W*c*) (Appendix). From these estimates, W*r* averaged 65% ± 1 of W*total* at Ta = 20–22°C, 64% ± 2 at Ta = 22–25°C and 67% ± 1at Ta = 25–27°C. For each of the three Ta ranges, W*total* of ESA1.5 and ESA5 scaled approximately to the 2/3 power of M (Fig. 7). In all instances, the slope of the allometric function of W*r* exceeded that of W*c*, on average by 13%. This difference is a mathematical consequence of the fact that, all factors being constant, surface specific-heat loss by radiation W*r*/m^2 is size-independent, while surface specific-natural convection W*c*/m^2 is inversely proportional to the 0.25 power of the animal's linear dimension (Appendix); hence, it must decrease with the increase in animal's size (Blaxter, 1989).

DISCUSSION

The question asked at the onset of the study was whether Tbs changed systematically with animal size. The answer is clearly negative, irrespective of the type of analysis adopted.

Methodological considerations

An effort was made to collect the data with the animal awake in the morning hours, to reduce the variability introduced by differences in the state of arousal and the circadian oscillation in heat dissipation (Aschoff, 1981; Shido et al., 1986; Briese, 1998). A few species included in the study, such as rat and mouse, are predominantly nocturnal; reanalysis of the data after elimination of these species had no impact on the linear regressions; therefore, the inclusion of these species has not modified the general conclusion.

The colour of the skin or pelt makes a difference only in the amount of heat accumulated under solar radiation, which has its peak within the visible spectrum, while it is irrelevant for radiant heat emitted; in fact, the dominant emitted wavelengths are in the infrared range, quite far from the visible spectrum. This is why the characteristically black and white stripes of a zebra or the dark and light areas of the coat of the giraffe are no longer distinguishable when assessed by infrared thermography in absence of sunlight (Cena and Clark, 1973). For the same reason, the emissivity ε has the identical value of 0.965 in the white-colored snow goose and the dark-colored Canada goose (Best, 1981), or the same value of 0.99 in the white-coloured snowshoe hares, and in brown-black sea otters and beavers (Hammel, 1956).

Comparison with previous data of skin temperature

Numerous data of skin temperature measured by thermocouples are available (e.g., Piccione et al., 2005; Roberts et al., 2010, for compilations). However, for the purpose of an estimate of the average Tbs, such measurements have limited use because, as indicated in the past (Folkow and Mercer, 1986), they provide data from arbitrarily selected regions and exclude the role of pelt coverage in determining the effective Tbs responsible for heat loss by radiation and convection.

More meaningful is the comparison of the current data with previous measurements of Tbs assessed by thermography. The Tbs of most body regions (legs, head, and trunk) in African and Indian elephants averaged, respectively, 23–24°C and 28–30°C (Williams, 1990). These latter values compare well with the 27.9 and 27.8°C recorded in the two African elephants of this study. In zebras and giraffes measured outdoors under clouded sky, Tbs averaged 29°C and 21.5°C, respectively (Cena and Clark, 1973). The former is close to the values measured in our two zebra specimens (29.7 and 30°C), but the giraffe's Tbs is some 10°C lower than that here observed, presumably because those data were collected at the Ta of 15°C under strong winds. Apart from physiological responses to the ambient conditions, which affect blood flow distribution to the skin, and the influence of Ta on Tbs (Phillips and Heath, 2001), measurements gathered outdoors can include the body heat accumulated by solar radiation (e.g., Fig. 2 in Norris et al., 2010). Hence, comparisons with previous data need to be assessed cautiously, especially when data were collected outdoors.

Tbs and the scaling pattern of heat loss

One of the best-documented allometric exponents in biology is that of metabolic rate; among adult mammalian species, it scales to the 0.75 power of body M (Peters, 1983, for review). Over the years, numerous interpretations have been offered for a mechanistic interpretation of the allometric scaling of metabolic rate in mammals (e.g., Schmidt-Nielsen, 1984; Dodds et al., 2001; Gillooly et al., 2001; West et al., 2002; Glazier, 2005). Irrespective of the mechanism responsible, as Tb bears no relation to body size, heat loss, and heat production must share a similar scaling pattern.

The present study was concerned specifically with the scaling pattern of Tbs and ESA, which, under our experimental conditions (constant Ta and no forced air convection) are the main factors responsible for heat loss by radiation and natural convection. The data showed that, when mammals are examined under identical ambient conditions, Tbs does not change systematically with body size, a conclusion that, of course, does not necessarily apply to values of Ta outside the 20–27°C range here investigated. The scaling pattern of ESA1.5 was quite close to 0.66, while that of ESA5 had a tendency to be slightly higher, on average ~0.72 and up to 0.75 (Fig. 6). From the experimentally obtained data of Tbs and ESA it was possible to estimate the heat loss by radiation and natural convection, according to standard laws of heat transfer applied to mammals (Blaxter, 1989); from these estimates, the scaling pattern of heat loss was quite close to the 2/3 power of M (Fig. 7). Hence, notwithstanding the assumptions and simplifications of the model (Appendix A), it would seem that under our experimental conditions heat loss by natural convection and radiation combined changes with animal's size less than metabolism does. However, this conclusion has many caveats.

The definition of the SA effectively engaged in heat loss is not without difficulties. In case of body regions facing or opposing each other, such as skin folds or plicae or the interior areas of the limbs, the heat radiated by one region can influence that opposite to it. The definition of the temperature gradient of physiological significance, which could vary from region to region, is somewhat arbitrary. In this study, we have chosen two temperature gradients, 1.5 and 5°C. Major regional differences in radiant heat dissipation are apparent even at a superficial look of the thermographs (e.g., Fig. 1) and are indicated numerically by the large coefficients of variation (Fig. 3) and the non-normal distributions of Tbs. Although in most animals the head is one of the main body districts for heat dissipation (Fig. 4), some mammals have preferential regions for heat transfer, such as the tail in some rodents and the pinnae in elephants. In fact, several investigators (Weissenböck et al., 2010; Norris et al., 2010) have pointed out that heat transfer operates through 'thermal windows' generated mainly by differences in local blood flow. When ESA comprises regions with only1.5°C difference from ambient temperature (ESA1.5), it closely corresponds to SA and its allometric exponent is close to 0.66. It is interesting that the exponent tended to increase for ESA5. This trend should signify that larger species have a relatively larger fraction of SA with high Tbs. Previously, Phillips and Heath (1995) measured ESA1.5 in 29 mammals during warm and cold conditions, and found that ESA1.5 varied more in larger than in smaller species; hence, the authors concluded that changes in ESA were the main mechanism adopted by large species to change body heat radiation. The current experiment, with ambient temperature maintained as constant as possible, was not designed to examine that possibility; nevertheless, the finding that the highest allometric exponent (0.75) occurred at the highest of the three ambient temperatures tested (Fig. 6) could be taken as in agreement with Phillips and Heath's (1995) proposition. The allometric exponent of the estimated heat loss (~0.66), lower than that of metabolic rate (0.75), would agree with the recent suggestion (Speakman and Król, 2010) that heat dissipation is the limiting factor to metabolic rate and, as mammals increase in size, the safety margin against hyperthermia decreases.

As mentioned in the Introduction, because pulmonary ventilation scales to $M^{0.75}$ (Stahl, 1967), it is probable that the evaporation through the respiratory tract scales at a similar exponent, but there is no information regarding the scaling pattern of cutaneous evaporation. Heat loss by conduction is limited to the contact to the ground; in the current study, all animals were standing, but it is possible that contact to the ground was relatively higher in the smallest specimens with shorter legs. Heat dispersion by convection may vary greatly among animals even in conditions of still air. For example, the flapping of the elephant's ears or the tail wagging of horses and other ungulates favours convection by stirring air boundary layers; the respiratory acts themselves can favor air convection from body surface, but the importance of these body movements in heat transfer, and the scaling pattern of their effects, is very difficult to evaluate.

Conclusion

Under the same environmental conditions and for the ranges of ambient temperature explored (between 20 and 27°C), Tbs is essentially body-size independent, whether one considers the total body surface or the effective surface areas. Therefore, systematic (size-dependent) differences in Tbs do not contribute to the differences in M-specific heat loss among mammals. It is possible that the fraction of body surface area devoted to heat radiation is slightly higher in larger species.

Appendix

The emitted radiant energy corresponds to

$$Wr = \sigma \cdot F\varepsilon \cdot A \cdot (Tbs^4 – Ta^4), \qquad (1)$$

where W*r* is the radiant heat in W (joules/sec), σ is the Stefan-Boltzmann constant ($5.67 \cdot 10^{-8}$ $W \cdot m^{-2} \cdot K^{-4}$), and Fε is the emittance factor which combines the emissivities of animal and surroundings (Blaxter, 1989). In this experiment, A is the animal's total surface area SA (m^2) or the effective surface areas (ESA1.5 and ESA5), computed as indicated in Methods. Tbs and Ta are, respectively, the absolute temperatures (°K) of the body surface and ambient. By assuming a spherical shape for both container and animal, the larger the ratio of the respective linear dimensions the more Fε approaches the value of the animal's ε; eventually, Fε almost corresponds to the animal's ε for ratios > 4 (Blaxter, 1989). Because ratios ≥ 4 were the most common situations of the present measurements, in (1) Fε was given the value of the animal's ε.

The loss of heat by natural convection from cylinders approximating the dimensions of the animals corresponds to

$$Wc = A \cdot (1.40 / L^{0.25}) \cdot (Tbs – Ta)^{1.25} \qquad (2)$$

(Blaxter, 1989), where W*c* is the heat convection in W (joules/sec). The characteristic dimension L corresponds to the diameter of the horizontal cylinder, and relates to the animal's body mass M (g) by the power function $L = 0.0064 \cdot M^{0.3506}$.

It follows from (1) that W*r*/A depends solely on the Tbs-Ta difference; therefore, it is body size-independent. In contrast, from (2) it is apparent that W*c*/A is inversely related to $L^{0.25}$; hence, with all other factors maintained constant, W*c*/A decreases, and the W*r*-W*c* ratio increases, with an increase in animal's size.

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