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Scaling the amplitudes of the circadian pattern of resting oxygen consumption, body temperature and heart rate in mammals

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Abstract

We questioned whether the amplitudes of the circadian pattern of body temperature (T_b), oxygen consumption ($\dot{V}_{O_2}$) and heart rate (HR) changed systematically among species of different body weight (W). Because bodies of large mass have a greater heat capacitance than those of smaller mass, if the relative amplitude (i.e., amplitude/mean value) of metabolic rate was constant, one would expect the T_b oscillation to decrease with the increase in the species W. We compiled data of T_b, $\dot{V}_{O_2}$ and HR from a literature survey of over 200 studies that investigated the circadian pattern of these parameters. Monotremata, Marsupials and Chiroptera, were excluded because of their characteristically low metabolic rate and T_b. The peak-trough ratios of $\dot{V}_{O_2}$ (42 species) and HR (35 species) averaged, respectively, 1.57±0.08, and 1.35±0.07, and were independent of W. The daily high values of T_b did not change, while the daily low T_b values slightly increased, with the species W; hence, the high-low T_b difference (57 species) decreased with W (3.3 °C $\cdot$ $W^{-0.13}$). However, the decrease in T_b amplitude with W was much less than expected from physical principles, and the high-low T_b ratio remained significantly above unity even in the largest mammals. Thus, it appears that in mammals, despite the huge differences in physical characteristics, the amplitude of the circadian pattern is a fixed (for $\dot{V}_{O_2}$ and HR), or almost fixed (for T_b), fraction of the 24-h mean value. Presumably, the amplitudes of the oscillations are controlled parameters of physiological significance.

Keywords: Allometry; Body temperature; Circadian patterns; Control of breathing; Control of heart rate; Metabolic rate; Oxygen consumption; Thermoregulation

1. Introduction

In mammals, an inner clock located in the brain suprachiasmatic regions controls the circadian patterns of many physiological events. Body temperature (T_b) and metabolic rate have robust circadian patterns, which in turn, either directly or indirectly, influence the daily patterns of many other functions (Refinetti, 2000). To what extent the amplitude of the circadian pattern is a fixed proportion of the mean value among species of different body size has rarely been considered. Specifically, in this study we consider T_b, oxygen consumption ($\dot{V}_{O_2}$), a variable that influences T_b, and heart rate (HR), which is sensitive to both T_b and $\dot{V}_{O_2}$.

Aschoff (1982) surveyed literature data for 20 species and suggested that the amplitude of circadian changes in T_b decreased with the increase in body weight (W). This relationship is expected if one considers that a large body mass implies a large heat capacitance. Hence, if all mammals had similar daily oscillations in specific metabolic rate, i.e., if the amplitude of the oscillation in metabolic rate was a fixed proportion of its mean value, the amplitude of the T_b oscillation should be greater in small, than in large, species. This interspecies difference would be further exaggerated if the oscillation of metabolic rate decreased with the increase in animal size, as originally proposed (Aschoff, 1982).

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However, a later literature survey covering 23 species did not confirm the earlier conclusion that the circadian amplitude of T_b dropped with the species *W* (Refinetti and Menaker, 1992). Another negative result emerged from an experimental study of 11 small species, ranging from 60 to 600 g (Refinetti, 1999), although the large inter-animal variability and the limited range in body size may have precluded a significant finding. Because heat dissipation, and not only heat production, contributes to the daily oscillation in T_b (Shido et al., 1986; Briese, 1998), the possibility exists that animals may either promote (large species) or limit (small species) heat loss to reduce the physical effects of the differences in heat capacitance and body surface-mass ratio. Whether or not the amplitude of the daily oscillations in HR may change systematically with *W* has never been looked at, and should depend on the corresponding patterns of T_b and metabolic rate.

During the last 20 years, the abundance of metabolic measurements and the advent of telemetry as common means for recording T_b and HR have provided a wealth of new data in numerous species. Therefore, the main aim of this study was to test the hypothesis that the amplitudes of the daily oscillations of T_b, $\dot{V}_{O_2}$ and HR may change systematically with the species *W*, by surveying the literature data pertinent to more than 50 mammalian species.

2. Methods

2.1. Literature survey

In the process of gathering data from the literature we excluded Monotremata, Marsupials and Chiroptera, because of their characteristically low metabolic rate and T_b. We excluded also data from animals with daily torpor or in hibernation. Data had to be collected with the animal at rest, preferentially at ambient temperatures between 20 and 25 °C (mean of all studies surveyed 24 °C±0.3). We did not consider data collected under conditions of large daily oscillations in ambient temperature, as it is often the case of field studies.

Ninety-four per cent of the studies examined were conducted under a light–dark regime of at least 7 h per phase, while a few (6%) were in free-running conditions (constant darkness). When several studies were available for any particular species, we gave preference to those with continuous recordings for several days. Following these criteria, 125 studies on 57 species of nine mammalian orders have been selected for the T_b data, 26 studies covering 42 species of six orders for the $\dot{V}_{O_2}$ data, and 35 studies on 20 species of six orders for the HR data (Tables 1–3). The results of all studies on any particular species were averaged together, to avoid undue bias toward those species more investigated.

In 71% of the studies surveyed for T_b, data had been recorded continuously by telemetry, by a transmitter often (61% of the cases) implanted in the abdomen. In the remaining 29% of the studies, data were collected at finite time intervals, most commonly from rectal probes. For the measurements of $\dot{V}_{O_2}$, 74% of the studies surveyed used an open circuit methodology with the animal undisturbed in a cage. In the remaining cases, measurements were obtained with closed circuit systems, at various time intervals. HR, most commonly (74% of the studies), was monitored by telemetry from implanted electrodes, while in the remaining cases data were obtained by auscultation or electrocardiography. Hence, the former methodology provided continuous data, the latter provided data at finite time intervals.

When the daily averages and the *high* and *low* values or amplitudes were not explicitly mentioned by the authors, we calculated their values from the data provided in tabular or figure format. Because nocturnal species have cycles almost 180° out of phase from those of diurnal species, the terms *high* and *low* refer to the daily maxima and minima, irrespective of the chronological time of their occurrence. When not specifically provided by the authors, the body weight for a given species, according to age and gender, was taken from standard bibliographic references (e.g., Silva and Downing, 1995).

2.2. Statistical analysis

All data are presented as means±1 SEM, unless stated otherwise. The statistical significance of a correlation was tested by linear regression analysis. Exponents (*b*) and intercepts (*a*) of the allometric equations relating a variable *Y* to *W* were derived from the least-squares regression analysis of the log-transformed equation $Y=a \cdot W^b$.

In addition to the allometric analysis, the species were separated into two groups, according to their *W*, or according to the 24-h means of the parameter under consideration. Then, the ratios between *high* and *low* values were statistically compared between the two groups. Correlation coefficients (*r*), differences between slopes (*b*) and differences in *high–low* ratios between animals of large and small *W* were tested using a two-tailed *t*-test. A difference was considered statistically significant at the level of $P<0.05$.

3. Results

3.1. Body temperature

The circadian patterns of a few small-, medium-, and large-size species, expressed in percent of their 24-h mean value, are presented in Fig. 1. Table 1 summarises the daily *high* and *low* T_b values for the 57 eutherian species surveyed. Almost invariably, the *high* values occurred in

Table 1
Survey of literature data: daily high and low values of body temperature

Order and species name	*W*, g	T_b high–low, °C	Sources
Artiodactyla			
Cattle, domestic, *Bos taurus*	500 250	39.4–38.5	Araki et al., 1984, 1987; Bitman et al., 1984; Bligh and Harthoorn, 1965; Lefcourt and Adams, 1996; Piccione et al., 2004
Goat, domestic, *Capra hircus*	30 000	39.1–38.6	Piccione et al., 2003
Hippopotamus, *Hippopotamus amphibius*	2 300 000	36.5–35.8	unpublished
Llama, *Lama glama*	142 000	38.2–37.7	Bligh et al., 1975
Alpaca, *Lama pacos*	60 250	38.2–37.8	Bligh et al., 1975
Sheep, domestic, *Ovis aries*	35 250	40.0–38.7	Bligh and Harthoorn, 1965; Bligh et al., 1975; Hunsaker et al., 1977; Maloney and Mitchell, 1996; Mohr and Krzywanek, 1990
Pig, Vietnamese, *Sus scrofa*	100 500	38.7–38.1	Ingram and Legge, 1970; Ingram and Mount, 1973; Lord et al., 1999
Carnivora			
Dog, *Canis familiaris*	15 000	38.4–37.7	Marvin and Reese, 1986; Rawson et al., 1965
Cat, *Felis catus*	3750	38.6–38.0	Kuwabara et al., 1986; Johnson and Randall, 1985; Randall et al., 1985
Fennec, *Fennecus zerda*	1000	38.5–37.3	Noll-Banholzer, 1979
Mongoose, slender, *Herpestes sanguineus*	540	39.2–37.3	Kamau et al., 1979
Coatimundis, *Nasua nasua*	3850	38.3–37.4	Chevillard-Hugot et al., 1980
Insectivora			
Tree Shrew, Northern, *Tupaia belangeri*	193	39.7–36.3	Refinetti, 1999
Lagomorpha			
Pika, Afghan, *Ochotona rufescens*	195	39.1–38.9	Luo et al., 1996
Rabbit, *Oryctolagus cuniculus*	1888	39.6–39.1	Akita et al., 2002; Luo et al., 1996; Varosi et al., 1990
Rodentia			
Mouse, spiny, *Acomys cahirinus*	65	38.2–36.3	Haim and Zisapel, 1999
Mouse, golden, *Acomys russatus*	71	37.8–36.2	Rubal et al., 1992
Mouse, field, *Apodemus mystacinus*	34	38.9–37.5	Rubal et al., 1992
Mouse, Nile, *Arvicanthis niloticus*	105	38.3–36.5	Blanchong et al., 1999; McElhinny et al., 1997
Guinea pig, *Cavia porcellus*	677	39.3–39.03	Akita et al., 2001; unpublished
Hamster, European, *Cricetus cricetus*	265	38.1–37.0	Wollnik and Schmidt, 1995
Prairie dog, black-tailed, *Cynomys ludovicianus*	1001	38.8–35.4	Reinking et al., 1977
Mole rat, African, *Georychus capensis*	236	36.6–35.3	Lovegrove and Muir, 1996
Woodchuck, Southern, *Marmota monax*	4300	38.2–37.4	Hayes, 1976
Gerbil, Mongolian, *Meriones unguiculatus*	63	38.1–36.2	Refinetti, 1996a
Hamster, Syrian, *Mesocricetus auratus*	158	38.1–36.8	Gao et al., 1991; Conn et al., 1990; Decoursey et al., 1998; Pickard et al., 1984; Refinetti et al., 1992; Refinetti, 1996a; Tang et al., 1999
Mouse, house, *Mus musculus*	32	37.7–36.0	Connolly and Lynch, 1983; Fuller et al., 2000; Hotz et al., 1987; Kluger et al., 1990; Yunis et al., 1974; Mousel et al., 2001; Nelson et al., 1975; Tankersley et al., 2002; Weinert and Waterhouse, 1999
Muskrat, *Obdatra zybethicus*	850	38.9–37.9	MacArthur, 1979
Degus, Chilean, *Octodon degus*	240	37.5–36.4	Kas and Edgar, 1998,2001; Refinetti, 1996a,b
Gerbil, fat-tailed, *Pachyuromys duprasi*	84	38.0–35.5	Refinetti, 1999
Mouse, white-footed, *Peromyscus leucopus*	33	38.5–35.6	Duffy et al., 1987
Mouse, deer, *Peromyscus polionotus*	14	38.3–36.2	Smith and Criss, 1967
Rat, *Rattus norvegicus*	281	37.9–36.6	Briese, 1985; Cahill and Ehret, 1982; Harkin et al., 2002; Honma and Hiroshige, 1978; Mortola and Seifert, 2000; Kittrell and Satinoff, 1986; Kluger et al., 1990; Lewis et al., 1986; Luo et al., 1996; Meinrath and D'Amato, 1979; Morley et al., 1990; Refinetti, 1996a, 1999; Refinetti et al., 1990; Satinoff et al., 1982; Scales and Kluger, 1987; Sei et al., 1997; Seifert et al., 2000; Seifert and Mortola, 2002a,b,c; Shido et al., 1989; Shiromani et al., 1991; Spencer et al., 1976
Mouse, pouched, *Saccostomus campestris*	94	36.6–34.7	Haim et al., 1988; Lovegrove and Raman, 1998
Squirrel, gr. europ., *Sciurus vulgaris*	300	38.3–35.6	Hut et al., 2002

(continued on next page)

Table 1 (*continued*)

Order and species name	W, g	T_b high–low, °C	Sources
Rodentia			
Mole rat, blind, *Spalax eherenbergi*	196	36.8–35.6	Goldman et al., 1997
Squirrel, golden, *Spermophilus lateralis*	250	40.0–37.0	Freeman and Zucker, 2000
Squirrel, Richardson, *Spermophilus richardsonii*	487	38.0–36.1	Refinetti, 1996a; Wang, 1972
Squirrel, thirteen l., *Spermophilus tridecemlineatus*	170	37.3–33.9	Refinetti, 1996a
Chipmunk, Eastern, *Tamias striatus*	95	39.8–37.3	Decoursey et al., 1998
Squirrel, flying, *Glaucomys volans*	74	37.0–35.5	Refinetti, 1999
Perissodactyla			
Donkey, *Equus asinus*	169 167	38.4–36.7	Maloiy, 1971; Yousef and Dill, 1969; Schmidt-Nielsen et al., 1957
Horse, *Equus caballus*	643 333	37.6–37.1	Evans et al., 1976; Piccione et al., 2002; Stull and Rodiek, 2000
Primates			
Night (owl) monkey, *Aotus trivirgatus*	1015	38.2–37.0	Hoban et al., 1985
Marmoset, common, *Callithrix jacchus*	400	38.3–35.8	Petry and Maier, 1990
Marmoset, pigmy, *Cebuella pygmea*	105	38.0–35.0	Morrison and Middleton, 1967
Cebus monkey, *Cebus albifrons*	1000	38.5–36.0	Winget et al., 1968
Man, *Homo sapiens*	68 382	37.2–36.4	Baehr et al., 2000; Hildebrandt, 1982; Kräuchi and Wirz-Justice, 1994; Little and Rummel, 1971; Nguyen and Tokura, 2002; Štefikova et al., 1986; Stephenson et al., 2000; Timbal et al., 1972; Wright et al., 1997
Cynomolgous, *Macaca fascicularis*	5000	37.4–35.2	Almirall et al., 2001
Macaque, rhesus, *Macaca mulatta*	4460	38.4–36.7	Crowley et al., 1972; Fuller et al., 1996; Hammel et al., 1963; Liu et al., 1981; Tapp and Natelson, 1989
Macaque, pigtail, *Macaca nemestrina*	6000	37.7–36.6	Reite and Short, 1980
Macaque, bonnet, *Macaca radiata*	4994	38.7–37.5	Reite and Short, 1986
Lemur, mouse, *Microcebus myoxinus*	32	37.8–34.0	Schmid et al., 2000
Baboon, jellow, *Papio cynocephalus*	10 000	38.7–37.1	Morishima and Gale, 1972
Squirrel monkey, *Saimiri sciureus*	971	38.5–36.4	Fuller, 1984; Fuller et al., 1979, 1985; Moore-Ede et al., 1977; Robinson et al., 1993; Sulzman et al., 1978; Wexler and Moore-Ede, 1986
Proboscidea			
Elephant, Indian, *Elephas maximus indicus*	5 000 000	35.7–35.2	Yathiraj et al., 1992
Xenarthra			
Armadillo, *Dasypus novemcinctus*	3400	36.5–34.5	Harlow et al., 1982

the evening hours (7–10 pm) and the *low* values in the early morning hours (7–10 am). The *high* evening values persisted throughout the night in nocturnal species, whereas they decreased in diurnal species (Fig. 1). Conversely, the *low* morning values in diurnal species increased throughout the day until the evening peak, whereas in nocturnal species they remained low for the most part of the day hours.

The allometric curve of the *high* values had no significant slope, and the average for all species was 38.2 °C±0.1. On the other hand, the *low* T_b values had a small, yet significant, correlation with W (35.6 $°C \cdot W^{0.004}$, $SD_{(b)}$=0.0015, r=0.32, P<0.02) (Fig. 2, top). Hence, the *high-low* difference in T_b decreased significantly with the increase in W (3.35 $°C \cdot W^{-0.13}$, $SD_{(b)}$=0.0249, r=0.57, P<0.001), from about 2 °C in the species of 10–10^3 g to about 0.5 °C in the species of 0.1–1 ton (Fig. 2, bottom). If all the rodents were eliminated, limiting the analysis to the remaining 31 species, the results of the allometric analysis would not change appreciably, and the *high-low* T_b difference would still drop slightly with W (4.0 $°C \cdot W^{-0.14}$, $SD_{(b)}$=0.0375, r=0.58, P<0.01). In the species of small body size (10^1–10^4 g), the daily *high* T_b values exceeded the *low* T_b values by 5.2%±0.4, whereas in the large species (10^4–10^7 g) the *high* T_b values exceeded the *low* T_b values by only 2%±0.3. This difference between large and small species was statistically significant (P<0.001). None of these allometric patterns showed any significant difference between predominantly nocturnal or diurnal species.

3.2. Oxygen consumption

Clear morning–evening differences in $\dot{V}_{O_2}$ had been reported in all the species surveyed, with the exception of the pocket gopher (Table 2). The allometric curves of the amplitude of the circadian pattern of $\dot{V}_{O_2}$ (0.042 ml/min$\cdot W^{0.62}$, $SD_{(b)}$=0.095, r=0.71, P<0.001) and of its daily average value (0.013 ml/min$\cdot W^{0.66}$, $SD_{(b)}$=0.031, r=0.96, P<0.001) run parallel to each other (Fig. 3). In fact, the

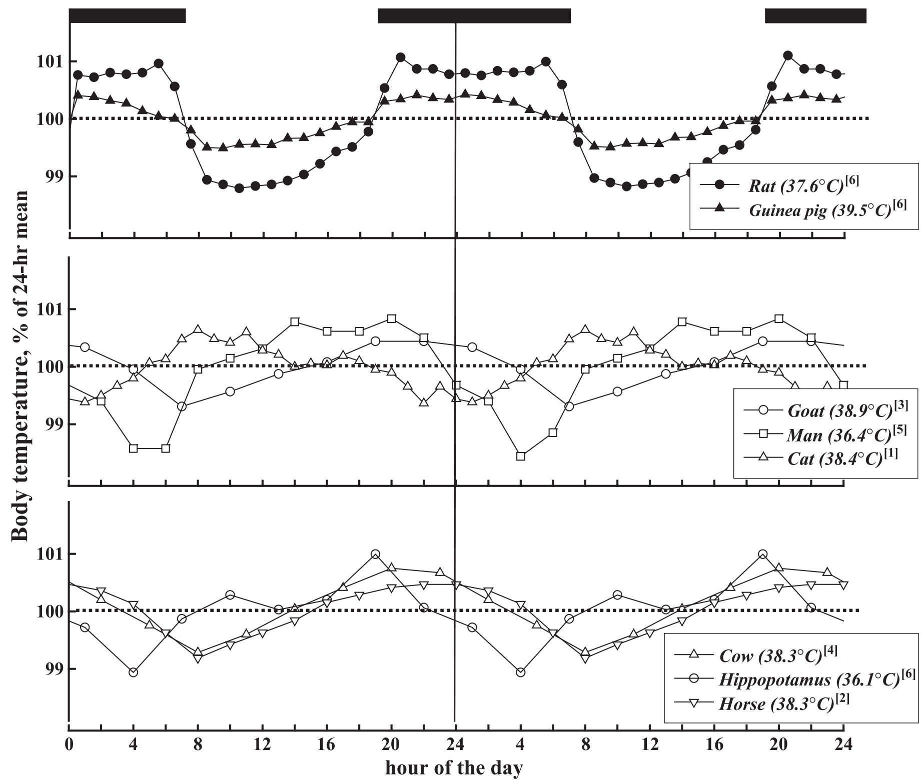

Fig. 1. Double-plot representation of the circadian pattern of body temperature in some small-, medium-, and large-size species, expressed in percent of their 24-h mean value (indicated in brackets). Filled symbols refer to the predominantly nocturnal species. [1]Johnson and Randall (1985). [2]Piccione et al. (2002). [3]Piccione et al. (2003). [4]Piccione et al. (2004). [5]Štefikova et al. (1986). [6]Present study, by telemetry with data loggers.

two exponents did not differ significantly, indicating that the relative amplitude of the circadian oscillation of $\dot{V}_{O_2}$ (amplitude/mean) was an interspecies constant. On average, the *high-low* $\dot{V}_{O_2}$ ratio for all species was 1.57±0.08, with no significant difference between the 28 species of small W (1–10^2 g: 1.56±0.09) and the 14 species of large W (10^2–10^6 g: 1.59±0.15). Equally, there was no significant difference in the *high–low* ratio between species with small or large $\dot{V}_{O_2}$ daily values.

3.3. Heart rate

The allometric curve of the *high–low* difference in heart rate ($320 \cdot W^{-0.28}$, $SD_{(b)}$=0.05, r=0.79, P<0.001) had a slope not significantly different from that of the daily average ($1076 \cdot W^{-0.24}$, $SD_{(b)}$=0.02, r=0.95, P<0.001) (Fig. 4). The lack of significant difference between the two slopes means that the oscillation was a constant fraction of the mean. This conclusion is also supported by the fact that the ratio between the *high* and *low* HR values (Table 3) did not differ significantly between the 13 species of small W (10^0–10^3 g: 1.36±0.10) and the seven species of large W (10^3–10^7 g: 1.33±0.09), the overall average being 1.35±0.07. Equally, there was no significant difference in the *high–low* ratio between the species with high daily values of HR and those with low daily values of HR.

4. Discussion

4.1. T_b and $\dot{V}_{O_2}$

The results of the allometric analysis of the *low* and *high* T_b values agree with Aschoff's original proposition (Aschoff, 1982) that the daily oscillation in T_b decreases in amplitude with the increase in animal W. This conclusion remained unaltered after exclusion of the rodents, to eliminate the possibility that some members of this order may have been studied in a semi-torpor state, which would have magnified their T_b oscillation.

At first glance, this result could be explained on physical grounds, since the larger body mass increases the heat capacitance, limiting the T_b swing in comparison to smaller species. However, several considerations make this explanation not very convincing. In fact, in a damped system the amplitude of the oscillation is reduced around its mean. Hence, if the larger heat capacitance was the main reason for the smaller T_b oscillation in the larger species one would have expected a reduction of the *high* T_b values, and an increase of the *low* T_b values, by a similar magnitude. This is not what we found, since only the *low*, not the *high*, T_b values significantly correlated with W. Furthermore, if the daily oscillation in T_b was simply the consequence of the daily oscillation in metabolic rate, the dampening of the T_b oscillation with the increase in animal

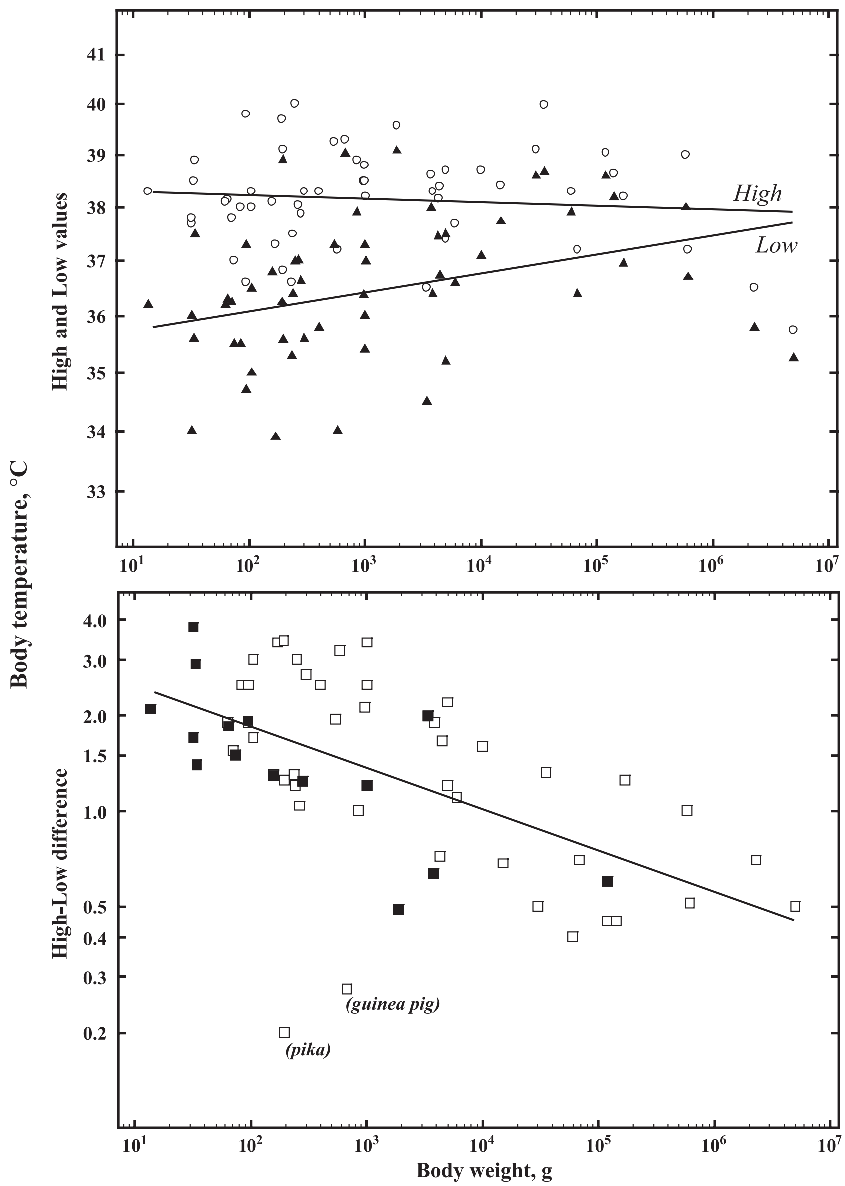

Fig. 2. Daily *high* and *low* values of body temperature (top panel) and their difference (bottom panel) in 57 species of eutherian mammals against the corresponding body weight (W, in log scale). Each symbol is the average value of one species (Table 1). In the top panel, continuous lines are the best-fit linear regressions. In the bottom panel, filled symbols refer to strictly nocturnal species, open symbols to diurnal, or also diurnal, species. Guinea pigs and pikas had unusually small oscillations of body temperature.

W should have been much more marked than observed. In fact, by geometrically comparing an animal to a sphere, the mass of which is directly proportional to heat production and the surface to heat loss, a rat-sphere of 200 g would have a radius of 3.6 cm, a surface of 163 cm^2, and a surface/volume ratio of 163/200=0.81 cm^{-1}, while a 2-ton hippo-sphere would have a radius of 78.2 cm, a surface of 76807 cm^2, and a surface/volume ratio of 76807/2000000=0.038 cm^{-1}. Therefore, the fourfold increase in W from the 200-g rat to the 2-ton hippo would lower the surface-mass ratio to 0.038/0.81, or less than 5% of the rat's value. This implies that the time constant of heat dissipation would be >20 times longer, damping the amplitude of the oscillation to <5%. Hence, if the amplitude of the T_b oscillation was strictly a physical phenomenon, in an animal the size of the hippo or the elephant the T_b oscillations should be <5% of the rat's oscillation, or about 0.05 °C; this is almost one order of magnitude less than actually measured. If physical properties were the major determinant of the T_b oscillations, the allometric scaling of the *high–low* difference in T_b should be as that of the SA/W ratio, or $W^{-0.33}$, whereas the actual exponent ($W^{-0.13}$, Fig. 2, bottom) was 2.5 times lower. Aschoff (1982) noted that some of the big species presented unexpectedly wide fluctuations in T_b, although those data may have been exaggerated by the large swings in ambient temperature. Subsequent studies in the cow and the horse under controlled ambient conditions have

Table 2
Survey of literature data: daily *high* and *low* values of resting oxygen consumption

Order and species name	*W*, g	$\dot{V}_{O_2}$ *high–low* ml/kg/min	Sources
Carnivora			
Mongoose, slender, *Herpestes sanguineus*	540	18.3–10.3	Kamau et al., 1979
Coatimundis, *Nasua nasua*	3850	10.0–5.0	Chevillard-Hugot et al., 1980
Insectivora			
Shrew, Short-tailed, *Blarina brevicauda*	20	167–95	Morrison, 1948; Randolph, 1980b
Mole, Western, *Scapanus orarius*	61	18–17	Kenagi and Vleck, 1982
Mole, Townsend's, *Scapanus townsendii*	138	17–14	Kenagi and Vleck, 1982
Shrew, masked, *Sorex cinereus*	8	123–116	Kenagi and Vleck, 1982
Shrew, Long-tailed, *Sorex dispar*	4	332–182	Morrison, 1948
Perissodactyla			
Donkey, *Equus asinus*	173 750	3.9–3.1	Maloiy, 1971; Yousef and Dill, 1969
Primates			
Man, *Homo sapiens*	73 340	4.2–3.7	Bosco et al., 2003; Kräuchi and Wirz-Justice, 1994; Little and Rummel, 1971; Timbal et al., 1972; Vargas et al., 2001
Lemur, mouse, *Microcebus myoxinus*	32	52.0–31.3	Schmid et al., 2000
Squirrel monkey, *Saimiri sciureus*	1075	15.2–9.9	Fuller et al., 1985; Robinson et al., 1993
Rodentia			
Mouse, spiny, *Acomys cahirinus*	65	24–17	Haim and Zisapel, 1999
Mouse, golden spiny, *Acomys russatus*	71	21–13	Rubal et al., 1992
Squirrel, antelope, *Ammospermophilus leucurus*	113	35–15	Kenagi and Vleck, 1982
Mouse, broad-toothed field, *Apodemus mystacinus*	34	60–39	Rubal et al., 1992
Guinea pig, *Cavia porcellus*	705	14–12	unpublished
Mouse, red-backed, *Clethrionomys gapperi*	24	77–48	Morrison, 1948
Kangaroo rat, desert, *Dipodomys deserti*	107	17–13	Kenagi and Vleck, 1982
Kangaroo rat, Merriam's, *Dipodomys merriami*	43	25–16	Kenagi and Vleck, 1982
Kangaroo rat, Ord's, *Dipodomys ordii*	49	24–20	Kenagi and Vleck, 1982
Gerbil, Mongolian, *Meriones unguiculatus*	72	36–32	Raab and Brady, 1976
Vole, long-tailed, *Microtus longicaudatus*	41	31–28	Kenagi and Vleck, 1982
Vole, meadow, *Microtus pennsylvanicus*	32	88–38	Morrison, 1948
Vole, Townsend's, *Microtus townsendii*	52	29–26	Kenagi and Vleck, 1982
Mouse, house, *Mus musculus*	18	79–48	Morrison, 1948
Wood rat, *Neotoma cinerea*	158	19–13	Kenagi and Vleck, 1982
Mouse, pocket, little, *Perognatus longimembris*	8	37–20	Kenagi and Vleck, 1982
Mouse, pocket, great basin, *Perognatus parvus*	19	32–30	Kenagi and Vleck, 1982
Mouse, deer, *Peromyscus crinitus*	14	35–22	Kenagi and Vleck, 1982
Mouse, white footed, *Peromyscus leucopus*	21	112–56	Morrison, 1948; Randolph, 1980a
Mouse, deer, *Peromyscus maniculatus*	18	62–32	Kenagi and Vleck, 1982; Morrison, 1948
Rat, *Rattus norvegicus*	219	32–24	Seifert and Mortola, 2002a,b,c
Mouse, pouched, *Saccostomus campestris*	94	37–35	Haim et al., 1988
Squirrel, golden, *Spermophilus lateralis*	259	18–10	Kenagi and Vleck, 1982
Chipmunk, yellow-pine, *Tamias amoenus*	53	29–24	Kenagi and Vleck, 1982
Chipmunk, least, *Tamias minimus*	34	45–26	Kenagi and Vleck, 1982
Chipmunk, Eastern, *Tamias striatus*	20	101–69	Randolph, 1980a
Pocket gopher, Botta, *Thomomys bottae*	232	23–23	Vleck, 1979
Pocket gopher, Northern, *Thomomys talpoides*	83	24–24	Kenagi and Vleck, 1982
Squirrel, flying, *Glaucomys volans*	70	62–19	Morrison, 1948
Mouse, pine, *Pitymys pinetorum*	23	90–60	Morrison, 1948
Xenarthra			
Armadillo, *Dasypus novemcinctus*	3400	14.2–4.7	Harlow et al., 1982

Values are the means of all the sources indicated. *high*, *low*: maximal and minimal values of the daily oscillation in resting oxygen consumption.

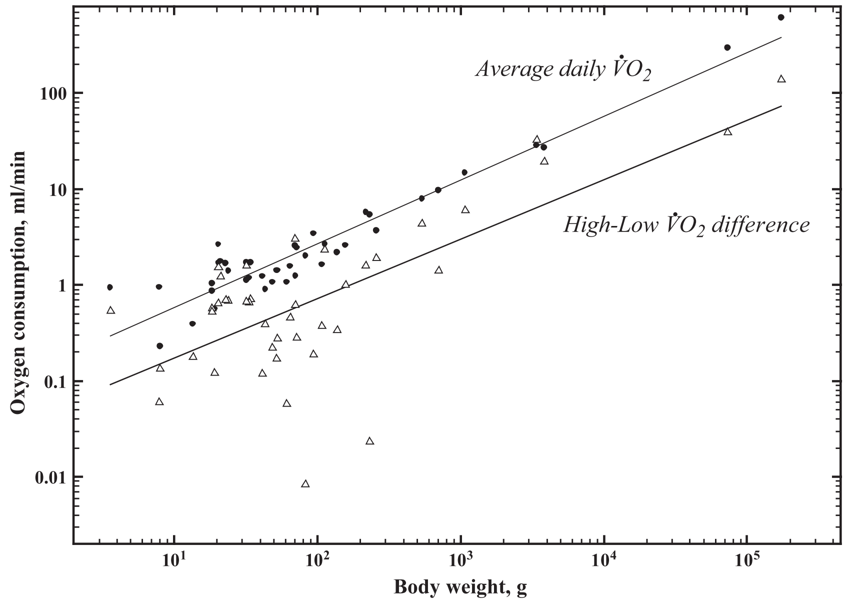

Fig. 3. Allometric relationship of the average daily oxygen consumption ($\dot{V}_{O_2}$, filled symbols) and of its *high–low* difference (open triangles) in 42 species of eutherian mammals. Each symbol is the average value of one species (Table 2). The oblique lines are the best fit linear regressions through the data points. The slopes of the two lines did not differ significantly.

confirmed the existence of significant (about 0.5 °C) T_b oscillations (Araki et al., 1984; Piccione et al., 2002, 2004).

The fact that the T_b oscillation in large animals is much greater than expected on physical principles could be attributed to a greater thermal conductance, or to wider oscillations in metabolic rate. However, neither is true. In fact, the W-specific thermal conductance in mammals not only does not increase, but actually decreases with the increase in W (Scholander et al., 1950; Aschoff, 1981). With respect to $\dot{V}_{O_2}$, the present allometric analysis has indicated that the $\dot{V}_{O_2}$ oscillation is a constant faction of the mean value.

In conclusion, the T_b oscillation decreased with W, but not nearly as much as one would have expected strictly on physical grounds. This must imply that, during the falling phase of metabolism and T_b, large animals promote heat dissipation more actively than smaller species do. Heat dissipation is known to present a circadian pattern (Aschoff, 1981; Shido et al., 1986; Briese, 1998), but inter-species comparative data are not available.

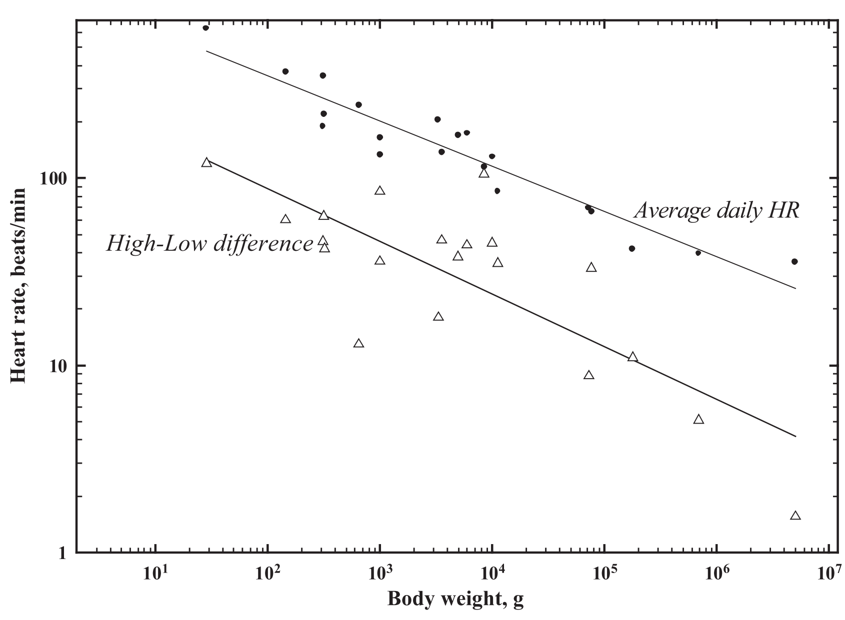

Fig. 4. Allometric relationship of the average daily value of heart rate (HR, filled symbols) and of its *high–low* difference (open triangles) in 20 species of eutherian mammals. Each symbol is the average value of one species (Table 3). The oblique lines are the best-fit linear regressions through the data points. The slopes of the two lines did not differ significantly.

Table 3
Survey of literature data: daily *high* and *low* values of resting heart rate

Order and species name	*W*, g	HR *high–low* beats/min	Sources
Carnivora			
Dog, *Canis familiaris*	11 200	105–70	Matsunaga et al., 2001
Fennec, *Fennecus zerda*	1000	148–112	Noll-Banholzer, 1979
Badger, *Taxidea taxus*	8500	175–70	Harlow, 1981
Black bear, *Ursus americanus*	76 600	78–45	Folk, 1967
Lagomorpha			
Rabbit, *Oryctolagus cuniculus*	3300	211–193	Akita et al., 2002
Perissodactyla			
Donkey, *Equus asinus*	177 500	46–35	Yousef and Dill, 1969
Horse, *Equus caballus*	690 000	42–37	Evans et al., 1976
Primata			
Cebus monkey, *Celebus albifrons*	1000	210–125	Winget et al., 1968
Man, *Homo sapiens*	72 088	74–65	Bosco et al., 2003; Kerkhof et al., 1998; Kräuchi and Wirz-Justice, 1994; Little and Rummel, 1971; van Dongen et al., 2001; Vargas et al., 2001; Wertheimer et al., 1974; Winget et al., 1974
Macaque, rhesus, *Macaca mulatta*	3575	165–119	Fuller et al., 1996; Malinow et al., 1974
Macaque, bonnet, *Macaca radiata*	4994	189–151	Reite and Short, 1986
Pigtail macaque, *Macaca nemestrina*	6000	196–152	Reite and Short, 1980
Baboon, *Papio*	10 000	150–105	Morishima and Gale, 1972
Tamarin, saddle back, *Saguinus fusciculis*	310	210–164	Hampton, 1973
Tamarin, cotton top, *Saguinus oedipus*	320	240–198	Hampton, 1973
Proboscidea			
Elephant, Indian, *Elephas maximus indicus*	5 000 000	36–35	Yathiraj et al., 1992
Rodentia			
Guinea pig, *Cavia porcellus*	650	254–241	Akita et al., 2001
Hamster, *Mesocricetus auratus*	145	440–380	Refinetti and Menaker, 1993
Mouse, house, *Mus musculus*	29	686–566	Tankersley et al., 2002
Rat, *Rattus norvegicus*	315	381–318	Zhang and Sannajust, 2000; Curtis et al., 2003; Harkin et al., 2002; Meinrath and D'Amato, 1979; Sei et al., 1997; Smith et al., 1987; van den Buuse, 1994; van den Buuse, 1999; Witte et al., 2000

Values are the means of all the sources indicated. *high*, *low*: maximal and minimal values of the daily oscillation in resting heart rate.

4.2. HR

The allometric function of the daily *high–low* difference in HR did not differ from that of the average HR, indicating that the amplitude of the oscillation of this variable is a fixed proportion of its daily mean. It would have been of interest to extend this analysis to breathing rate, but published data are very few. Circadian patterns of breathing rates have been reported for rats, cows and humans (Seifert and Mortola, 2002a; Vargas et al., 2001; Bosco et al., 2003; Piccione et al., 2004). From these data, all collected during wakefulness, one can calculate that the amplitude of the oscillation in breathing rate was 8% of the 24-h mean in the rat, 16% in humans, and 9% in the cow. In the elephant, where measurements were conducted only in the morning and in the evening, the difference was 6% of the mean (Yathiraj et al., 1992). We have measured breathing rates in a variety of medium and large-size specimens, including aquatic mammals, and found that the morning–evening differences were quite variable, with no correlation with the species *W* (unpublished observations). Hence, as for HR, it seems that also the relative amplitude of the breathing rate oscillation does not change systematically with the species W. Whether the same conclusion applies to cardiac output and pulmonary ventilation is impossible to say, because circadian measurements of tidal volume and stroke volume have been performed only in a few rodents (Smith et al., 1987; Seifert and Mortola, 2002a; Mortola, 2004).

4.3. Conclusions

At the onset of the study we asked whether the amplitudes of the daily oscillations in $\dot{V}_{O_2}$, T_b, and HR decreased systematically with the species W. For $\dot{V}_{O_2}$ and HR the answer is a negative one. In fact, scaling analysis indicated that the oscillations are a fixed percentage of the 24-h means. With respect to T_b, the daily oscillation decreased significantly with W, but the drop was considerably less than expected solely on physical principles. This implies that mechanisms controlling heat loss, favouring it in large species and limiting it in small species, operate to maintain the T_b oscillation within a narrow limit. The amplitude of the T_b oscillation has been considered a key mechanism for the central clock to synchronise and control the peripheral functions (Brown et al., 2002). Hence, the control of its amplitude within narrow limits would be an important regulatory requirement.

The presence of a biological clock is a fundamental aspect of life at all levels of organisation. Yet, the daily oscillations of physiological variables and functions required for time-keeping could jeopardise the needs for stability and homeostasis. Presumably, the control of the amplitude of the oscillations, despite the physical and physiological differences introduced by the large variations in body size, represents a compromise between the requirements for time-keeping and the needs for inner stability.

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