Corrections to the proofs of
"Temperature-associated upper limits to body size in terrestrial poikilotherms"
by Makarieva, Gorshkov and Li

1) Page 1, authors' affiliation, third line
"- MM and B.-L. Li" should be changed to "- AMM and B.-L. Li"

2) Splitting Table 1 into columns should be as follows (column borders are shown for clarity sake):
Essentially, symbols N_W, T_Y, T_M, T_{MIN}, N_{GB}, L_{GB}, N_A, L_A should be at the same level (i.e. vertically aligned).

Taxon	Common name	N_W	Largest in the world Range; reference location	T_Y, T_M, T_{MIN} (°C)	Largest in Great Britain	N_{GB}	L_{GB} (cm)	Largest on Wrangel Island	N_A	L_A (cm)
INSECTA:										
Collembola	Springtails	7 000	*Paralobella orousetti* Philippines; Manila	27, 29, 20	*Tomocerus longicornis*	400	0.6	*Isotoma gorodkovi*	33	0.3
Etc.										

3) Table 1, Notes, 5th line
"(Eq. 5);Sources" should be changed to "(Eq. 5); Sources"

Table 1, Notes, 1st line
"Notes:L_W" should be changed to "Notes: L_W"

Table 1, Notes, 4th line
"respectively;[a]Body" should be changed to "respectively; [a]Body"

4) **IMPORTANT!!!**

For some reason, the original Eq. (6) disappeared from the text, while Eq. (7) is given twice, at its own place and instead of Eq. (6). The correct Eq. (6) is:

$$\log\left(\frac{L_1}{L_2}\right) = \frac{1}{\gamma}\log\left(\frac{N_1}{N_2}\right), \quad \frac{L_1}{L_2} = \left(R_N\right)^{\frac{1}{\gamma}}, \tag{6}$$

5) Page 8, right column, bottom line
"In these organisms" should be changed to "In such organisms"

6) Page 10, right column, 11th line from bottom
"animals-mammals-biochemically" should be changed to "animals - mammals - biochemically"

7) REFERENCES
Page 5, right column, bottom line:
(Babenko et al. 1997) should be changed to (Babenko and Bulavintsev 1997)
this solves the problem of the uncited reference and the missing reference Babenko et al. 1997 in the reference list

Reference details:
Peters, R. H. 1983. The ecological implications of body size. - Cambridge University.
West, G. B., Brown, J. H. and Enquist, B. J. 1997. A general model for the origin of allometric scaling laws in biology. - Science 276: 122-126.

8) APPENDIX
Notes to Table 1, second line from bottom.

"in Appendix." should be changed to "in Appendix, which can be obtained from the authors."
Or any other appropriate note should be inserted (e.g. "published on OIKOS electronic site"? with an address).

Temperature-associated upper limits to body size in terrestrial poikilotherms

Anastassia M. Makarieva, Victor G. Gorshkov and Bai-Lian Li

Makarieva, A. M., Gorshkov, V. G. and Li, B.-L. 2005. Temperature-associated upper limits to body size in terrestrial poikilotherms. – Oikos 00: 1–12.

We show that the largest tropical species of terrestrial poikilotherms from 25 taxa exceed, in linear body size, the largest representatives of the same taxa from the temperate (e.g. Great Britain) and polar (e.g. Wrangel Island) zones by 3.2 and 5.7 times, respectively. Here we develop a theoretical approach which quantitatively explains the observed body size patterns and relates them to ambient temperature under the assumption that there exists a temperature-independent critical minimum value of mass-specific metabolic rate b_{min}, a fall below which is incompatible with successful biological performance. This value sets an upper limit to linear body size within a taxon. Mass-specific metabolic rate decreases with increasing body size but, in poikilotherms, grows exponentially with ambient temperature. Such compensation of the size-related drop in mass-specific metabolic rate b by higher ambient temperature extends the permitted range of body sizes for which $b \geq b_{min}$. As a result, the maximum linear body size grows approximately twofold per each ten degrees of increase in ambient temperature. We also discuss why this prediction does not apply to interspecific comparisons of aquatic poikilotherms, for which an opposite trend is to be expected. We quantify in theory the maximum body size patterns recently reported for benthic gammaridean amphipods.

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Within most taxa the whole-body metabolic rate B grows with body mass as $B \propto M^{\alpha}$, where $\alpha < 1$. This means that the mass-specific metabolic rate $b \equiv B/M$ is higher in small organisms and lower in large ones. Living organisms display a huge range of body sizes, from bacteria ($M \sim 10^{-12}$ g) to the largest mammals ($M \sim 10^{8}$ g). A typical value of $\alpha \approx 0.7$ would correspond to a 1 000 000-fold difference in mass-specific metabolic rates. Are such kind of differences indeed observed or is the corridor of mass-specific metabolic rate changes in fact much narrower, bounded by universal maximum and minimum values common for most taxa?

In a study of unicells, poikilotherms and homeotherms, Robinson et al. (1983) noted that if one considers the smallest representatives of each group, their mass-specific metabolic rates predicted by the scaling relationship empirically established for each group coincide with an accuracy of less than 10%, indicating a universal temperature- and size-independent upper limit to mass-specific metabolic rate. In mammals, Geiser (1988) demonstrated that the minimum mass-specific metabolic rate attained by hibernating mammals is similarly independent of body size. Singer et al. (1993) highlighted the temperature independence of this minimum value by showing that it coincides with the metabolic tolerance limit of hypothermia. That is, the minimum critical temperature the mammal can tolerate grows with increasing body size thus offsetting

the size-associated decrease in mass-specific metabolic rate.

Generally, however, little attention has been paid to investigating the absolute bounds within which the mass-specific metabolic rate changes with changing body size and temperature. Meanwhile it is likely that such research could provide clues to important ecological problems. For example, Makarieva et al. (2003) showed that several major patterns in population dynamics of plants could be explained assuming the existence of a universal minimum value b_{min} of mass-specific metabolic rate. The same assumption accounted for a diversity of other phenomena, including the breakpoint of body shape scaling in larger mammals and the decrease of ecosystem leaf area index with elevation.

In this paper we explore the temperature-associated patterns that can be predicted by assuming the existence of b_{min}. The value of b_{min} sets an upper limit to body size within each taxonomic group. Mass-specific metabolic rate decreases with increasing body size but, in poikilotherms, grows with ambient temperature. Compensation of the size-related drop in mass-specific metabolic rate by higher temperature extends the permitted range of body sizes for which $b \geq b_{min}$. Hence, the maximum body sizes attained by species inhabiting warmer environments should be larger than the maximum body sizes attained by species from the same taxon but living at lower temperatures.

We develop a theoretical framework which allows for a quantitative formulation of the above predictions and verify them by the available data for 25 taxa of terrestrial poikilotherms from the tropical, temperate and arctic zones. We also discuss the relevance of our approach to aquatic and homeothermic animals.

Rationale

Energy that supports life comes to the organism through some part of its body surface and is dissipated via body surface after it has been used up. Although there have been relatively few studies relating metabolic rate directly to body surface area, the available data summarised by Kooijman (2000, pp. 66–71) tend to support the assumption of proportionality between energy consumption rate and body surface area in various organisms (Jacobsen 2000). We can write therefore:

$$B \equiv bM = fS \tag{1}$$

In the steady state the animal consumes as much oxygen as is needed to metabolise the consumed food. Hence, the proportionality coefficient f in Eq. 1 describes both the flux of oxygen supply and the flux of energy uptake per unit area, depending on the units of measurements.

As is well-known, the functional dependence of mass-specific metabolic rate b on body size and temperature

T has the form of a product of temperature- and size-dependent terms, $b \alpha F_1(T)F_2(size)$. Function $F_1(T)$ is traditionally expressed in terms of the relative change per 10°C (Q_{10}): $F_1(T) \propto Q_{10}^{(T-T_0)/10°C}$, where T_0 is a reference temperature. We then have from Eq. 1:

$$b = f_0 Q_{10}^{(T-T_0)/10°C} \frac{S}{M} \tag{2}$$

The size- and temperature-independent proportionality coefficient f_0, defined for a reference temperature T_0, should be taxon-specific and reflect the modes of respiration and food uptake.

If body shape is conserved within a given taxon, we have $S \propto L^2$ and $M \propto L^3$, where L is a linear size of the organism, for example, body length. Then $S/M \propto L^{-1}$ and one obtains from Eq. 2,

$$L = \frac{f_0 Q_{10}^{(T-T_0)/10°C}}{b}, \quad L_{max} = \frac{f_0 Q_{10}^{(T-T_0)/10°C}}{b_{min}} \tag{3}$$

Maximum body size $L_{max}(T_1)$ of species living at temperature T_1 should therefore relate to the maximum body size $L_{max}(T_2)$ of species living at temperature T_2 as

$$R_L \equiv \frac{L_{max}(T_1)}{L_{max}(T_2)} = Q_{10}^{\Delta T/10°C} \tag{4}$$

where $\Delta T \equiv T_1 - T_2$. For a difference of 10°C in environmental temperatures one should observe a twofold difference in maximum linear body sizes assuming $Q_{10} = 2$.

In organisms with elongated cylindrical bodies, for which length L is much larger than diameter D, $L \gg D$ (e.g. worms) we have $M \propto LD^2$ and $S \propto LD$. In this case, body length L cancels from the ratio $S/M \propto D^{-1}$ in Eq. 3:

$$D_{max} = \frac{1}{b_{min}} f_0 Q_{10}^{(T-T_0)/10°C} \tag{5}$$

Interestingly, Eq. 5 essentially means that, under the assumptions made, there are no metabolic restrictions on body length in elongated organisms. This effect may provide an explanation for the fact that in some taxa of elongated organisms the longer bodies have a higher L/D ratio than the shorter ones. For example, while in the smaller nematodes a typical L/D ratio does not exceed 50 (Goodey 1963), the length record-holders, *Dracunculus medinensis* (L = 1.2 m) and *Placentonema gigantissima* (L up to 8.4 m), are exceptionally slim, with the L/D ratio of 1200 and 336, respectively (Gubanov 1951). However, other factors, including mechanical ones (e.g. resistance forces while burrowing in earthworms), should also be analysed when accounting for the body shape changes in different taxa.

We now aim to test the predicted ratios between maximum linear body sizes attained by species of a given taxon living at high, intermediate and low temperatures.

We confine the present consideration to taxa of terrestrial (air-breathing) poikilotherms.

Methods

Body size

According to Eq. 4, the largest representatives of each taxon should be found in the tropics, where temperature is the highest. We identified the world's largest species from 25 taxa and determined their geographic ranges (Table 1). As expected, all of them but one appeared to inhabit the tropics (Fig. 1). As a representative territory in the temperate zone we chose Great Britain, which possesses one of the best studied faunas. For the coldest environments we used the available faunistic descriptions of Wrangel Island (approx. 71°N, 179°W, Russia). Its whole territory ($22\,257$ km^2) is occupied by the state nature reserve "Wrangel Island", so the fauna of this territory is relatively well studied.

The choice of taxa was primarily determined by the availability of relevant literature and by the condition that they must be present in Great Britain, to allow for comparisons between different climatic zones. In most cases, we first sought for the candidates for the world's largest animal within each taxon in secondary literature and website articles. Then we looked for original scientific sources where body size measurements of the candidate species were reported and, on a comparative basis, chose the largest. Where a range of body sizes was reported, the upper value was used.

Several British authors pinpointed the largest British animal themselves. In the remaining cases, to identify the largest species we compared the available species descriptions and/or consulted professionals. Identification of the largest poikilotherms on Wrangel Island was based on the available species check-lists (Martynova et al. (1973) for springtails and Khruliova (1987) for the remaining taxa) and species keys. Only native and well established species were considered.

Temperature

Most poikilotherms are active during the warmer part of the year. The prediction that we are testing is that the biological design of terrestrial poikilotherms is such that their mass-specific metabolic rate does not go below b_{min}. As long as the lowest values of metabolic rate are to be observed at the lowest temperatures, the extreme minimum temperatures that animals encounter during their activity season are of particular interest for our analysis. We collected data on mean annual temperature, mean daily temperature of the warmest month and extreme minimum temperature of the warmest month for Great Britain, Wrangel Island and territories in-

habited by the world's largest poikilotherms (Table 1). A reference location for which climatic tables were available was chosen for each world's largest species, either in the centre of its geographic range or in the nearest vicinity of a reported sampling location. For Great Britain, the reported temperatures correspond to the inland climate of England. All climatic data come from Landsberg (1969–1984), except for Oceania (Lebedev and Yegorova 1974).

Results

Body size differences versus ambient temperature

The results are summarised in Table 2. On average, the world's largest poikilotherms from the studied taxa are 3.2 and 5.7 times longer than their counterparts from Great Britain and Wrangel Island, respectively, while largest poikilotherms in Great Britain are 2.0 times longer than on Wrangel Island.

Extreme minimum temperatures T_{MIN} of the warmest month constitute on average 18°C for the world's largest poikilotherms and 6°C and -5°C for Great Britain and Wrangel Island, respectively. Theoretically predicted ratios R_L of maximum linear body sizes that are obtained from Eq. 4 using the corresponding temperature differences ΔT_{MIN} and a typical value of $Q_{10} = 2$ agree well with the observed values. In the World-Great Britain comparison the observed R_L ratio is better described by $Q_{10} = 2.5$ (an upper estimate of commonly observed Q_{10} values, Table 2).

Body size differences vs species numbers

Before reaching the conclusion about a satisfactory agreement between the theory and observations, it is necessary to sort out the species number issue. The maximum body size in a small random sample of species from a taxon is smaller than the maximum body size in the entire taxon. Could this statistical effect account for the observed drop of maximum body sizes in the local faunas of Great Britain and Wrangel Island?

For a variety of taxa May (1978) showed that, to the right of the mode, the spectral density of species numbers per unit logarithmic interval of body size decreases proportionally to $L^{-\gamma}$, where $\gamma \approx 2$ (Fig. 2). Assuming that the modal species density N_{max} is proportional to the total number of species in the sample, $N_{max} \propto N$, it is easy to estimate the mean ratio between maximum body sizes, L_1 and L_2, attained within the entire taxon with N_1 species and in a random sample of $N_2 \leq N_1$ species from the same taxon, respectively. On a log-log scale the value of γ is equal to the tangent of angle ϑ the species distribution line

Table 1. Maximum body sizes in terrestrial poikilotherms living at different latitudes

Taxon	Common name	N_W	Largest in the world Range; reference location	T_Y, T_M, T_{MIN} (°C)	L_W (cm)	Largest in Great Britain	N_{GB}	L_{GB} (cm)	Largest on Wrangel Island	N_A	L_A (cm)
INSECTA: Collembola	springtails	7 000	*Paralobella orousetti* Philippines; Manila	27, 29, 20	1.5	*Tomocerus longicornis*	400	0.6	*Isotoma gorodkovi*	33	0.3
Dermaptera	earwigs	1 000	*Labidura herculeana* St. Helen Island; Jamestown	22, 25, 19	7.8[a]	*Forficula auricularia*	5	2.3[a]			
Orthoptera	grasshoppers[b]	20 000	*Macrolyristes imperator* Malaysia; Singapore	27, 28, 21	12	*Tettigonia viridissima*	33	5.5			
Blattodea	cockroaches	4 000	*Macropanesthia rhinoceros* Queensland AU; Townsville	24, 28, 19	7.5	*Blatta orlentalis*	4	2.5			
Heteroptera	bugs	31 000	*Lethocerus maximus* South America; Rio De Janeiro	23, 26, 17	11.0	*Ranatra linearis*	525	3.0	*Chiloxanthus stellatus*	4	0.83
Odonata: Anisoptera	dragonflies	2 400	*Petalura ingentissima* Queensland AU; Townsville	24, 28, 19	16.2[c]	*Anax imperator*	17	10[c]			
Odonata: Zygoptera	damselflies	2 500	*Megaloprepus caerulatus* C. and S. America; San José	20, 21, 12	20[c]	*Agrion virgo*	26	7.4[c]			
Lepidoptera: Rhopalocera	butterflies	24 000	*Ornithoptera alexandrae* Papua New Guinea; Madang	27, 28, 20	25[c]	*Papilio machaon*	111	9.5[c]	*Erebia fasciata*	12	6.0[c]
Lepidoptera: Heterocera	moths	136 000	*Thysania agrippina* Brazil; Recife	26, 27, 21	28[c]	*Acheronta atropos*	2 000	12.7[c]	*Dicallomera kusnezovi*	>23	4.5[c]
Coleoptera: Scarabaeoidea	scarab beetles	20 000	*Megasoma elephas* Mexico through Venezuela; Morelia	18, 21, 08	13.7	*Lucanus cervus*	68	7.5			
Coleoptera: Carabidae	ground beetles	32 000	*Mormolyce phyllodes* Malaysia, Java; Djakarta	27, 27, 21	7.8	*Carabus intricatus*	344	3.6	*Carabus truncaticollis*	17	1.9
Hymenoptera: Formicidae	ants	9 500	*Camponotus gigas* Malaysia, Borneo; Kuching	27, 28, 19	3.1[d]	*Formica sanguinea*	50	1.2[d]			
Hymenoptera: Apidae	bees	25 000	*Megachile pluto* Indonesia, North Moluccas; Menado	26, 27, 18	3.9	*Bombus terrestris*	267	2.2	*Bombus hyperboreus*	5	2.2
Hymenoptera: Pompilidae	spider wasps	5 000	*Pepsis heros* F. Brazil, Ecuador, Peru; Lima	18, 22, 15	5.4	*Priocnemis perturbator*	41	1.7			
Diptera: Nematocera	thread-horns		*Holorusia brobdingnagia* Northern China; Paotou	06, 23, 09	4.8[e]	*Tipula maxima*	2 080	3.0[e]	*Tipula arctica*	49	1.9[e]
Diptera: Brachycera	short-horns		*Gauromydas heros* Brazil; Recife	26, 27, 21	6.0	*Tabanus sudeticus*		2.5			
ARACHNIDA: Araneae	spiders	34 000	*Theraphosa* sp. Brazil; Recife	26, 27, 21	7.6	*Dolomedes* sp.	650	2.4	*Alopecosa hirtipes*	30	1.25
ARACHNIDA: Acari	mites, ticks	52 500	*Dinothrombium tinctorium* Guinea coast of Africa[f]; Conakry	27, 28, 20	1.6	*Trombidium holosericeum*	1 720	0.5			
CHILOPODA	centipedes	2 800	*Scolopendra gigantea* Mexico through Venezuela; Maracaibo	28, 29, 20	30	*Haplophilus subterraneus*	40	7.0			
DIPLOPODA	millipedes	10 000	*Archispirostreptus gigas* Kenya; Mombasa	27, 29, 21	28	*Cylindroiulus londinensis*	52	4.8			
GASTROPODA: Styllomatophora	land snails	35 000	*Achatina achatina* Nigeria; Lagos	26, 28, 19	27[g]	*Helix pomatia*	87	4.5[g]			

Table 1 (*Continued*)

Taxon	Common name	N_W	Largest in the world Range; reference location	T_Y, T_M, T_{MIN} (°C)	L_W (cm)	Largest in Great Britain	N_{GB}	L_{GB} (cm)	Largest on Wrangel Island	N_A	L_A (cm)
AMPHIBIA: Anura	frogs	4 900	*Conraua goliath* Cameroon; Douala	27, 28, 20	32	*Bufo bufo*	5	8.0			
REPTILIA: Serpentes	snakes	2 500	*Python reticulatus* Malaysia, Sumatra; Medan	26, 27, 18	900	*Natrix natrix*	3	170			
REPTILIA: Sauria	lizards	3 000	*Varanus komodoensis* Indonesia, Komodo Island; Kupang	27, 28, 20	313	*Anguis fragilis*	3	46			
OLIGOCHAETA: Lumbricina	earthworms	3 000	*Rhinodrilus fafner* Brazil; Recife	26, 27, 21	2.4 [h]	*Lumbricus terrestris*	35	1 [h]	*Eisenia nordenskioldi*	1	0.5 [h]

Notes:L_W, L_{GB}, L_A — largest linear body size (body length unless otherwise stated) attained within a taxon in the world (W), in Great Britain (GB), and on Wrangel Island (A[rctic]); T_Y, T_M, T_{MIN} — annual mean daily temperature (Y), mean daily temperature of the warmest month (M), extreme minimum temperature of the warmest month in the reference location (the lowest value recorded during the period of observations, usually 10–30 years) (MIN); T_Y, T_M, T_{MIN} for Great Britain and Wrangel Island are 10, 16, 6 and −12, 03, −5°C, respectively; N_W, N_{GB}, N_A — number of species in the considered taxon in the world, Great Britain, and on Wrangel Island, respectively;[a]Body length including forceps;[b]also crickets and bush crickets;[c]wingspan;[d]body length of queens;[e]wing length;[f]location of original description by Linneaus;[g]shell length;[h]body diameter (Eq. 5);Sources for body size, species ranges and species numbers are given in Appendix. In some cases only partial species range (typical location) is reported. Taxa with missing L_A values are either absent from Wrangel Island or the relevant data are unavailable.

makes with the horizontal axis (Fig. 2). Simple geometric considerations allow us to write:

$$L = \frac{f}{b_0 Q_{10}^{(T-T_0)/10°K}}, \quad L_{max} = \frac{f_{max}}{b_0 Q_{10}^{(T-T_0)/10°K}} \tag{6}$$

where $R_N \equiv N_1/N_2$.

For most of the taxa studied we collected data on the numbers of described species in the World, Great Britain and on Wrangel Island (Table 1). The log-log regression of the ratios L_W/L_{GB} and L_{GB}/L_A on the ratios N_W/N_{GB} and N_{GB}/N_A (a total of 32 points) produced a slope of $1/\gamma = 0.18 \pm 0.05$ ($r^2 = 0.29$, $p < 0.005$), which corresponds to $\gamma \approx 5.6$ (95% C.I. 3.6–12.5). That is, to explain the observed R_L ratios by differences in species numbers one has to adopt an assumption completely lacking empirical support, namely that the number of species in all samples drops with body size as $L^{-5.6}$ instead of L^{-2} documented for global distributions (May 1978). Values of R_L predicted from Eq. 6 at $\gamma = 2$ appear to be up to one order of magnitude higher than the observed values (Table 2).

A closer inspection of the R_L–R_N plots suggests that the observed minor but statistically significant effect of species numbers is rapidly saturated with decreasing R_N (Fig. 3). At high R_N the ratio $R_L = L_W/L_{GB}$ for comparison between the World and Great Britain drops abruptly with decreasing $R_N = N_W/N_{GB}$. At lower R_N it remains approximately constant and close to the predicted value of $R_L = 2.3$. (Mathematically, this is manifested in the fact that when the six points with the largest $R_N \geq 300$ in Fig. 3, are removed, the $\log R_L$–$\log R_N$ regression of the remaining 17 points reveals no dependence of R_L on R_N: $1/\gamma = -0.04 \pm 0.11$, $r^2 = 0.01$). When the asymptotic predicted value of R_L is reached (which means that the metabolic upper limit to body size corresponding to a given temperature is attained), the analysis of larger territories and more species within the same climatic zone should not lead to any further reduction of the R_L ratio.

For example, for *Eisenia nordenskioldi*, the single and, by definition, largest earthworm on Wrangel Island, the R_L ratio, $L_{GB}/L_A = 2$, is close to the predicted value at $Q_{10} = 2$ (Table 2). Although it is in principle possible that if we had studied more species within the same climatic zone, we could have found worms larger than *E. nordenskioldi*, from $R_L = 2$ we predict that this species is not to be superseded in size by any other animal from the same taxon and climatic zone. And, indeed, Eisen (1879) states that *E. nordenskioldi* attains a size not equalled by any other earthworm from northern Europe and, in the warmer regions, loses only to *Lumbricus terrestris*, the largest earthworm of Great Britain. Similarly, *I. gorodkovi*, the largest springtail on Wrangel Island ($L_{GB}/L_A = 2$) exceeds in body size all polar desert species of Collembola found between 40° and 180° eastern longitude (Babenko et al. 1997). We conclude
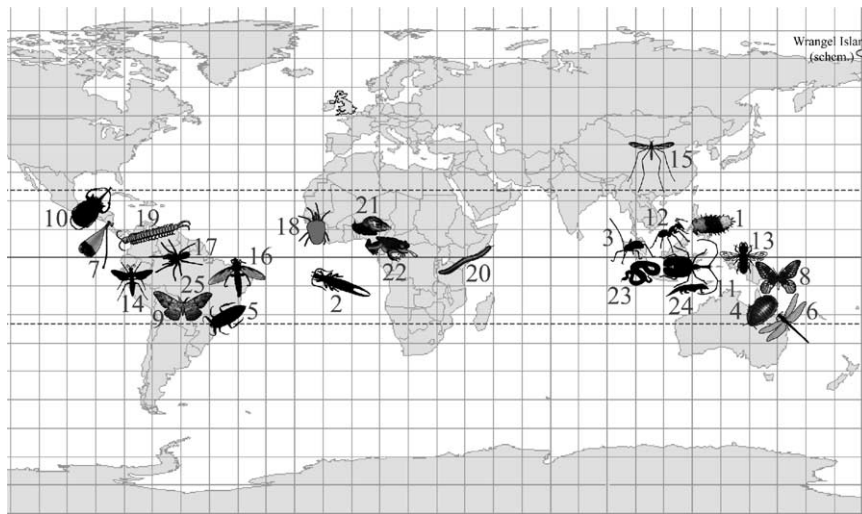
Fig. 1. The geography of world's largest terrestrial poikilotherms. Taxa are numbered as in Table 1. Species-denoting icons were prepared from original drawings or photos. Note that *H. brobdingnagia* is shown without forelegs as in the original as in the original figure of Westwood (1876). *R. fafner* is shown by number (25) only. Tropics are shown by the dashed lines. Wrangel Island is shown schematically (enlarged).

that although the effect of species numbers does not play a major role in the present analysis, it could possibly account for the abnormally high R_L ratios observed in several taxa.

Body size differences: aquatic and homeothermic animals

Aquatic environments are characterised by oxygen concentrations more than an order of magnitude lower than the atmosphere. Besides, due to the high viscosity of water, the coefficient of eddy diffusion which governs such respiration-related processes like ventilation is about four orders of magnitude lower in water than in the air. Hence, while in terrestrial poikilotherms the oxygen flux f (cf. Eq. 1 and 2), grows readily with temperature, enhancing oxygen supply in response to the rising ambient temperature poses a serious problem for aquatic organisms. Mass-specific metabolic rate $b(T) \geq b_{min}$ rises exponentially with increasing temperature, $b(T) = b_0 Q_{10}^{(T-T_0)/10^\circ K}$. When $f = f_{max}$ cannot be further elevated, we obtain for aquatic organisms, (cf. Eq. 3):

$$L = \frac{f}{b_0 Q_{10}^{(T-T_0)/10^\circ K}}, \quad L_{max} = \frac{f_{max}}{b_0 Q_{10}^{(T-T_0)/10^\circ K}} \quad (7)$$

This means that, in contrast to terrestrial poikilotherms, the largest aquatic poikilotherms should be larger at lower temperatures and smaller at higher ones. For example, the world's longest worm (*Lineus longissimus*), largest medusa (*Cyanea arctica*), second largest shark (*Cetorhinus maximus*) are regularly found in British waters, as well as further to the north. In the meantime, none of the British terrestrial poikilotherms claims to be world's largest (Table 1). This is an additional argument against a role for species numbers in the temperature-associated body size patterns. In spite of the fact that species numbers increase towards the equator in terrestrial as well as in aquatic taxa (Rex et al. 2000), terrestrial and aquatic poikilotherms appear to display opposing geographic body size trends.

A mechanism similar to the one underlying Eq. 7 was proposed to explain the intraspecific pattern that many poikilotherms grow smaller at higher temperatures (Atkinson 1994). If the rate of oxygen diffusion into the living cell is largely independent of temperature, then at higher temperature the cell has to become smaller to

Table 2. Differences in maximum linear body sizes versus differences in environmental temperatures and species numbers in terrestrial poikilotherms living at different latitudes

Comparison	n	R_N	ΔT_{MIN}	R_L observed		R_L predicted from		
			(°C)	range	mean ± sd	Eq. 4 at $Q_{10}=2$	Eq. 4 at $Q_{10}=2.5$	Eq. 6 at $\gamma=2$
World — Great Britain	25	300	12	1.6...6.8	3.2 ± 1.4	2.3	3.0	17
Great Britain — Wrangel Island	9	46	11	1.0...3.6	2.0 ± 0.8	2.1	2.7	6.8
World — Wrangel Island	9	3400	23	2.5...13.3	5.7 ± 3.0	4.9	8.2	58

Notes: n — number of taxa used in the comparison. R_N — ratio between species numbers in a given taxon (Table 1, column 2, 5, 7) in the compared territories averaged over all taxa. For example, $R_N = 300$ means that the world's number of species in the considered 25 taxa is on average 300 times higher than in Great Britain. ΔT_{MIN} — difference in the extreme minimum temperatures of the warmest month between the considered territories. R_L observed — ratio of maximum linear body sizes L in a given taxon between the compared territories averaged over all taxa.
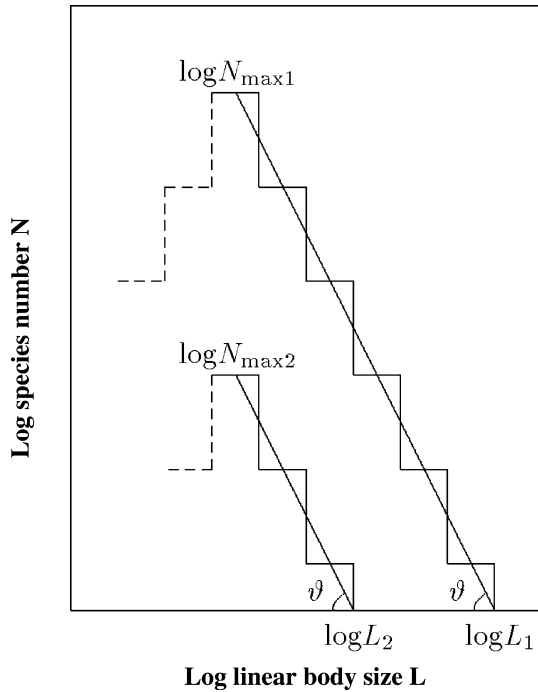
Fig. 2. Maximum body sizes vs species numbers. The larger histogram shows a model distribution of global species numbers over body size in a taxon with a total of N_1 species; lower histogram shows a similar distribution in a random sample of $N_2 < N_1$ species from the same taxon; L_1 and L_2 are the maximum body sizes and $N_{max1} \propto N_1$ and $N_{max2} \propto N_2$ are the maximum spectral densities of species numbers attained in the two distributions.
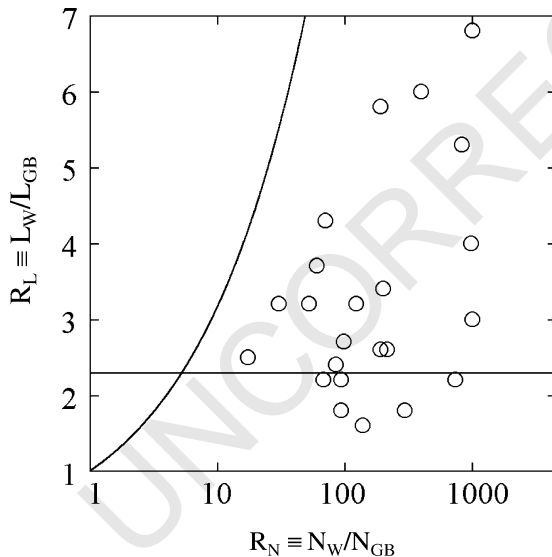

Fig. 3. Ratio $R_L \equiv L_W/L_{GB}$ between maximum linear body sizes versus ratio $R_N \equiv N_W/N_{GB}$ between species numbers in the considered taxa in the world (W) and Great Britain (GB). Horizontal line: $R_L = 2.3$ (Table 2); curve: $R_L = R_N^{1/2}$ (Eq. 8).

cope with its oxygen demands (Woods 1999). We now consider the problem of whole-organism vs cellular oxygen supply in greater detail.

Let m, s and n_c be cell mass, surface area and number, respectively, so that total body mass M equals n_c m; f_c be diffusion flux of oxygen per unit cell surface area. Body surface S and body mass M are generally related as $S = k(M/\rho)^{2/3}$, where ρ is density (kg m^{-3}) and k is a dimensionless geometric coefficient reflecting body shape. For simplicity, here we put both ρ and k equal to unity, so that $S = M^{2/3}$ for the whole organism and $s = m^{2/3}$ for the cell. For a single cell we can write $bm = f_c s$, so that $bm^{1/3} = f_c$. For the whole organism $bM^{1/3} = f$, where f is the rate of oxygen supply per unit body surface area. We thus have

$$\frac{f}{M^{1/3}} = b = \frac{f_c}{m^{1/3}} \tag{8}$$

We now discuss three body size patterns; (a) intraspecific comparisons of organisms reared or living at different temperatures, (b) interspecific comparisons of aquatic organisms living at different ambient temperatures, and (c) interspecific comparisons of air-breathing organisms living at different ambient temperatures.

(a) The value of f_c is determined by species-specific cell properties, e.g. membrane biochemistry. Diffusion flux f_c is only weakly dependent on temperature and should be approximately the same in conspecific organisms reared at high and low temperatures. If mass-specific metabolic rate b grows with ambient temperature, $b(T_2) > b(T_1)$, $T_2 > T_1$, at constant f_c (or in the case of f_c growing more slowly with temperature than does b) this means that in order to maintain energy budget (Eq. 8), the cell must become smaller, i.e. $m(T_2) < m(T_1)$. Each tissue and organ in the organism are designed to perform some meaningful function. Tissue architecture, including the number of cells of which the tissues and organs are composed, are programmed by the species genome. Hence, the number of cells n_c cannot vary freely with ambient temperature. At constant n_c and diminishing m, total body mass $M = n_c$ m will also drop at high temperature in intraspecific comparisons.

(b) In interspecific comparisons f_c does not need to be conserved, neither does the total number of cells n_c. In this case the right-hand equality in Eq. 8 does not impose any constraint on total body mass M. However, in aquatic organisms the oxygen flux per unit body surface area $f = f_{max}$ can be limited by the low concentration of the dissolved oxygen (Eq. 7). If b grows with increasing temperature, while f does not, the only way for maintaining the energy budget, see the left-hand equality in Eq. 8, is to reduce body mass M at higher temperatures.

Thus, the possible decrease of body mass at higher temperatures within species and between aquatic species is due to the approximate temperature-independence of

fluxes f_c and f, respectively. However, the reasons for this temperature-independence are different; f is limited by low ambient oxygen concentration, while f_c is relatively independent of temperature as a diffusion flux.

(c) Finally, in air-breathing organisms enjoying very high oxygen concentrations f can readily grow with increasing temperature to match any energetic demands of the organism, $f(T_2) > f(T_1)$, $T_2 > T_1$. Different species of air-breathing poikilotherms can therefore afford being large at high temperatures, $M(T_2) > M(T_1)$, still keeping their mass-specific metabolic rate b above the critical value b_{min}.

Moreover, if geographically different populations of one and the same air-breathing species are metabolically adapted to different temperatures, i.e. have a similar $b = const$, then, due to the possibility of increasing f at high temperature, the air-breathing organisms can be bigger at high temperatures at the same time featuring a constant species-specific f_c and constant m (Eq. 8). Hence, for intraspecific comparisons of air-breathing organisms both larger and smaller body sizes at high temperatures are possible, corresponding to $b = const$ (large f, large M, large n_c, constant m and f_c) and $n_c = const$ (large b, small M, small m, constant f and f_c), respectively. (For intraspecific comparisons of aquatic organisms the first pattern cancels due to the impossibility of rising f with increasing temperature, Eq. 7). Accordingly, Blanckenhorn and Demont (2004) found that in intraspecific comparisons of terrestrial arthropods Bergmann's rule and converse Bergmann's rule (i.e. body size increasing or decreasing with increasing latitude) are approximately equally probable.

Assuming that the value of f_{max} is dictated by oxygen availability and, hence, is proportional to concentration $[O_2]$ of water dissolved oxygen (Peck and Chapelle 1999), one can predict from Eq. 7 the magnitude of maximum body length change with changing environmental temperature and oxygen concentration. Based on a survey of 1853 species of benthic amphipods, Chapelle and Peck (1999, 2004) observed that maximum body length increases with concentration of dissolved oxygen, but decreases with ambient temperature. For example, world's largest amphipods come from lake Baikal ($T_{Ba} = 6°C$, $[O_2]_{Ba} \approx 400$ µmol kg^{-1}), measure $L_{Ba} = 54.4$ mm in length and are 7.8 times longer than the largest amphipods of tropical areas with $L_{Tr} = 4$ mm, $T_{Tr} = 25°C$ and $[O_2]_{Tr} \approx 200$ µmol kg^{-1} (Chapelle and Peck 1999). Assuming $f_{max} \propto [O_2]$, the corresponding ratio R_L predicted from Eq. 7 at $Q_{10} = 2$ is

$$R_L = \frac{L_{Ba}}{L_{Tr}} = \frac{[O_2]_{Ba}/[O_2]_{Tr}}{2^{(T_{Ba} - T_{Tr})/10°K}} = 7.5 \qquad (9)$$

falling close to the observed value of 7.8. At $Q_{10} = 2$ temperature difference alone ($\Delta T = T_{Ba} - T_{Tr} = 19°C$) could have explained only a 3.7-fold difference in maximum body size, while the difference in oxygen

concentration alone could have explained an approximately twofold difference in maximum body size. Temperature and oxygen effects combined quantitatively account for the observed maximum body size change in amphipods.

Generally, flux f of oxygen supply via body surface is proportional to the product of diffusion coefficient d (note that this can be a coefficient of either turbulent or molecular diffusion) and oxygen concentration $[O_2]$. In the above consideration we assumed d to be temperature-independent. However, the pattern of larger body sizes at lower temperatures is expected to be observed in aquatic invertebrates even if d would grow with temperature with a Q_{10} equal to or less than that of mass-specific metabolic rate b. In the case of equal Q_{10} for d and b, the corresponding body size difference will be solely determined by different concentrations of dissolved oxygen at different temperatures. In this case one could expect only a twofold difference between body lengths of amphipods living at the highest, $[O_2]_{Ba} \approx 400$ µmol kg^{-1}, and lowest, $[O_2]_{Tr} \approx 200$ µmol kg^{-1}, oxygen concentrations. Interestingly, the mode of amphipod body sizes studied by Chapelle and Peck (2004) changes only 2.6-fold within this range of oxygen concentrations (from approx. 4.2 mm in the tropics to approx. 11 mm in Baikal). This suggests that different constraints can be imposed on body sizes and metabolic rates of the medium-sized compared to the largest representatvies of the taxon.

Equation 7 may also provide a clue to the phenomenon of oxygen-dependent upper thermal tolerance: The critical maximum temperature an organism can tolerate increases with increasing availability of ambient oxygen. To meet the metabolic demand which grows exponentially with temperature (Eq. 7), the rate f of oxygen supply per unit body surface area should also grow. However, f is bounded by f_{max}. The temperature at which f reaches f_{max} becomes the critical one. As far as f_{max} grows with $[O_2]$, the critical maximum temperature should similarly grow with increasing $[O_2]$.

The principal difference between Eq. 3 and 7 for air-breathing and aquatic poikilotherms allows one to expect that the oxygen-dependent thermal tolerance is not to be consistently observed in terrestrial poikilotherms. Air-breathing organisms enjoying high ambient oxygen concentrations may have no problems with increasing oxygen supply with growing temperature, so for them the critical maximum temperature and oxygen availability can be unrelated. Insects, with their highly efficient tracheal system of oxygen delivery, will be the last to experience oxygen shortage with increasing temperature (Klok et al. 2004). At the other end of the scale are aquatic organisms suffering both from low oxygen concentration and from the lack of an efficient system of oxygen delivery. In these organisms the

oxygen-dependent thermal tolerance is to be observed most consistently.

In homeotherms maintaining a constant body temperature T_b the flux of heat release via body surface S is proportional to the difference between T_b and ambient temperature T, $f \propto T_b - T$. This allows one to write

$$b\frac{M}{S} \propto bL \propto T_b - T \quad \text{and} \quad L \propto \frac{T_b - T}{b} \quad (10)$$

If the value of b changes more slowly than the $T_b - T$ in comparisons between related species living at different characteristic ambient temperatures, Eq. 10 yields Bergmann's rule for homeotherms: related species of homeotherms should be larger at lower temperatures, i.e. at greater differences $T_b - T$.

Bumblebees, with their ability of keeping themselves warm in cold environments (Heinrich 1972), represent an intermediate case between terrestrial poikilotherms (small at low T) and homeotherms (large at low T). The two mutually compensating trends, Eq. 3 and 10, are likely to be responsible for the absence of difference ($R_L = 1$) in body sizes of the largest Apidae of Great Britain and Wrangel Island, Table 1.

Discussion

We have shown that the statement that there exists a temperature-independent minimum mass-specific metabolic rate b_{min} allows one to quantitatively explain the observed interspecific differences in maximum linear body sizes of terrestrial poikilotherms living at different temperatures.

For intraspecific comparisons it was proposed that smaller body sizes in terrestrial arthropods (e.g. insects) at high latitudes can be related to the shorter warm season (Chown and Gaston 1999, Blanckenhorn and Demont 2004), especially in larger species completing one generation per year. That is, organisms growing for a short time do not grow large. However, this consideration implicitly assumes that insect life cycle is limited to one year. In the meantime, nothing prevents high latitude species from extending their life cycle to many years. In this case, while they still would grow only a little during each season, in several seasons they could, in principle, reach the same adult body size as their temperate or tropical counterparts. And, indeed, insect species from cold environments and high latitudes much more often possess long life cycles (up to ten years and more) than temperate species (Danks 1992, Danks et al. 1994). This consideration shows that for interspecific comparisons, where life cycle length does not need to be conserved, season length does not impose any constraint on body size. Moreover, no quantitative theoretical approach has been developed to predict how changes in season length translate numerically into body size

changes. The idea of possible season length constraints on body size remains therefore a qualitative hypothesis, which, unlike the quantitative approach presented in this paper, cannot be numerically evaluated on the basis of the available empirical evidence.

It has been argued (Makarieva et al. 2003) that the minimum mass-specific metabolic rate $b_{min} > 0$ exists due to the need to compensate for the spontaneous breakdown of the highly-organised state of the living matter. However, under certain conditions the organism may choose not to protect itself continually, but let the damage accumulate for some time in order to repair it when the unfavourable period is over and normal metabolic rate is re-established. During freezing, extreme dehydration, prolonged anoxia or other periods of inactivity the living organisms may have no measurable metabolic rate at all, like, e.g. dry bacterial spores (Desser and Broda 1965). It is legitimate therefore to look for b_{min} during activity season, where the major properties of living matter (e.g. reproduction and energy exchange with the environment) are manifested and the corresponding structures need to be continuously protected from degradation.

Our approach makes use of the assumption that whole-body metabolic rate B scales proportionally to body surface S, $B \propto S$ (Eq. 1). This framework allows for a physically and biologically transparent interpretation of the involved variables, in particular, the energy (oxygen) flux f per unit body surface area. It also makes possible a straightforward expression of body size changes in terms of linear body size (Eq. 4 and 5). This is important, as far as namely linear body size is most frequently reported in species descriptions, while body mass estimates are often missing, especially in invertebrates.

For the case of geometric similarity, when $M \propto L^3$ and $S \propto L^2$, proportionality between B and S corresponds to a scaling exponent of $\mu = 1/3$ in the relationship between mass-specific metabolic rate and body mass $b \propto M^{-\mu}$. Two distributive network models proposed by West et al. (1997) and Banavar et al. (1999, 2002) would argue in favour of $\mu = 1/4$. However, Dodds et al. (2001) revealed that the model of Banavar et al. (1999) is mathematically controversial, as it demands that the volume V_d of distributive network scales as $V_d \propto L^{D+1}$ and at the same time as $V_d \propto M \propto L^D$, where L is body length and D is body dimensionality. The fundamental criticism of Dodds et al. (2001) has not been addressed in the follow-up paper by Banavar et al. (2002), where the controversy persists (Makarieva et al. 2005). The model of West et al. (1997) was similarly shown to suffer from fundamental drawbacks, including violation of the energy conservation law when applied to the ontogenetic growth problem (Makarieva et al. 2004), absence of predicative power at the ecosystem scale (Li et al. 2004), logical inconsistency and failure to be supported by empirical

evidence on a broad taxonomic scale (Makarieva et al. 2005). Hence, on theoretical grounds, there are no arguments for a scaling exponent different from the physically transparent $\mu = 1/3$ in the case of geometric similarity.

Generally, the fact that many observed scaling exponents μ are not equal to 1/3 has been often interpreted as evidence against proportionality between whole-body metabolic rate B and body surface S (Peters 1983). However, it is rarely appreciated that $\mu = 1/3$ follows from $B \propto S$ in the case of geometric similarity only. If geometric similarity is violated, i.e. when $M \propto L^x$, where $x \neq 3$, the proportionality between B and S can give rise to a great variety of scaling exponents μ, including the widely discussed case of $\mu = 1/4$. It is best illustrated on a concrete example.

Consider a flat-shaped organism, e.g. a bivalve, where the approximately isometric shell width and shell length D significantly exceed shell height L, $D \gg L$. Body surface of such an organism scales as $S \propto D^2$, while its body mass scales as $M \propto D^2L$. Suppose that among differently-sized bivalves there is no geometric similarity, i.e. $L \propto D^y$, where $y \neq 1$. Then for body mass M we have $M \propto D^{2+y}$ and for shell height L we have $L \propto D^y \propto M^{y/(2+y)}$. Now, using the assumption $B \propto S$ (Eq. 1), we obtain for mass-specific metabolic rate $b \equiv B/M \propto S/M$ that $b \propto 1/L \propto M^{-y/(2+y)}$, i.e. $\mu = y/(2+y)$. For example, in the bivalve *Yoldia hyperborea* dry body mass scales as $M \propto D^{2.55}$ (Stead and Thompson 2003). This gives $y = 0.55$ and predicts $\mu = y/(2+y) = 0.22$ (instead of $y = 1$ and $\mu = 1/3 = 0.33$ as would be in the case of geometric similarity). Experimentally measured mass-specific metabolic rate in this species scales as $M^{0.26}$, where M is dry mass (Stead and Thompson 2003), i.e. the observed $\mu = 0.26$ is very close to $\mu = 0.22$ predicted from Eq. 1.

To summarize, the physically transparent fundamental assumption of proportionality between whole-body metabolic rate B and body surface area S adopted in the present approach cannot be dismissed on the grounds that the observed scaling exponents μ may differ from 1/3. On the contrary, this assumption can quantitatively predict such exponents on the basis of the observed body shape changes between the compared organisms.

An interesting question is whether the observed dependence between body size and temperature is confined to maximum body sizes or pertains to mean body sizes as well. This would imply the existence not only of a minimum but also of an optimum temperature- and size-independent value of mass-specific metabolic rate (Gorshkov 1981, Gorshkov et al. 2000, Makarieva et al. 2005). That is, by choosing habitats and life styles with different environmental temperatures as dependent on their body size and changing accordingly their respiratory, digestive and circulatory systems (i.e. the f_0

values in Eq. 2), the organisms can evolve to keep their mass-specific metabolic rate near a universal optimum value b_{opt} common for all taxonomic groups (Makarieva et al. 2005). Below we briefly outline the available evidence justifying further investigations in this direction.

Almost two centuries ago, Kirby and Spence (1826) noted that tropical species of an insect genus usually exceed those of colder climates in size. More quantitatively, May (1978) estimated, based on the study of Schoener and Janzen (1968), that the mean body length of species from five insect orders is approximately 1.5-fold larger in the tropics than in the temperate zone. Looking from the opposite side, Strathdee and Bale (1998) pointed out that Arctic insects are typically smaller than related temperate species. Russian researchers extended this observation to the whole of the arctic ecosystems, including such taxa as nematodes, insects, spiders and functional groups like soil animals. A special term "miniaturisation of life" was coined to describe the observed poleward decrease of body size in various taxa (Chernov et al. 1979). In a study of 346 species Addo-Bediako et al. (2002) observed a statistically significant negative correlation between ambient temperature and body mass of insects with known metabolic rates.

In the larger terrestrial poikilotherms, the effect of compensation of a larger body size by higher environmental temperature is suggested by the study of mass-specific metabolic rate b_f in lizards measured in the field, which, according to Nagy et al. (1999), is nearly independent of body mass, $b_f \propto M^{-0.08}$. This scaling exponent is significantly smaller in absolute value than the corresponding scaling exponents of standard mass-specific metabolic rate, which in lizards range from -0.20 to -0.17 (Bennett and Dawson 1976). That is, b_f in lizards drops with body mass considerably more slowly than their standard mass-specific metabolic rate measured at a reference temperature. This can be explained if one assumes that the larger reptiles live in warmer environments. On a related note, Autumn et al. (1997) remark that while diurnal lizards come in all sizes (up to 150 kg), nocturnal lizards (i.e. those living at lower temperatures) are typically small (1–300 g).

On a macroscale, we note that the largest extant animals-mammals-biochemically exist at high temperatures of around 37°C. The evolutionary origin of homeothermy can be thus viewed as a compensation for the size-induced deviation from the optimum mass-specific metabolic rate in the largest animals. Recent research proposes a similar temperature-compensation mechanism for the largest dinosaurs (Seebacher et al. 1999, Singer et al. 1993). In a study of a large poikilotherm *Crocodylus porosus* it was shown that as the organism grows larger, it spends progressively more time in the air (e.g. basking) and less time in the water. Due to such

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behavioural thermoregulation, the mean body temperature grows with increasing body size of the animal and compensates for the size-related decrease in specific metabolic rate (Seebacher et al. 1999).

Finally, the developed theoretical approach highlighting the difference in temperature associated body-size patterns between the aquatic and terrestrial poikilotherms can be applied to the analysis of Bergmann's rule, especially at the interspecific level. It remains to be established whether the existing exceptions to Bergmann's rule in poikilotherms (Blackburn et al. 1999, Ashton and Feldman 2003) come predominantly from terrestrial taxa, as predicted from Eq. 3 if it written for the mean body sizes with b_{opt} instead of b_{min}.

Uncited reference

1) Babenko and Bulavintsev, 1997.

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