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Gigantism, temperature and metabolic rate in terrestrial poikilotherms

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The mechanisms dictating upper limits to animal body size are not well understood. We have analysed body length data for the largest representatives of 24 taxa of terrestrial poikilotherms from tropical, temperate and polar environments. We find that poikilothermic giants on land become two–three times shorter per each 10 degrees of decrease in ambient temperature. We quantify that this diminution of maximum body size accurately compensates the drop of metabolic rate dictated by lower temperature. This supports the idea that the upper limit to body size within each taxon can be set by a temperature-independent critical minimum value of mass-specific metabolic rate, a fall below which is not compatible with successful biological performance.

Keywords: body size; temperature; mass-specific metabolic rate; terrestrial poikilotherms; Great Britain; Wrangel Island

1. INTRODUCTION

The relationship between metabolic rate and body size has been predominantly studied in terms of body size as independent, and metabolic rate as dependent, variables and not vice versa, e.g. Peters (1983). However, several studies suggest that certain critical values of metabolic rate may set limits to animal body size. For example, in a study of unicells, poikilotherms and homeotherms, Robinson *et al.* (1983) noted the smallest representatives of each group have a nearly uniform mass-specific metabolic rate. This suggests that the smallest size within each group can be dictated by this uniform value of mass-specific metabolic rate. Geiser (1988) found that mammals hibernating at low body temperature reduce their metabolic rate down to approximately 0.1 W kg^{-1} irrespective of body size. Singer *et al.* (1993) suggested that the maximum body size in mammals is prescribed by this minimum value: as far as mass-specific metabolic rate decreases with growing body size, no further growth of body size is expected when this critical value is reached. Makarieva *et al.* (2003) proposed that the maximum amount of metabolically active biomass of plants attainable at a given ambient temperature and solar irradiance is similarly dictated by a minimum temperature-independent mass-specific metabolic rate $q_{\min}$ compatible with viability of living tissues.

In this paper we report evidence which further supports the idea that the upper limit to body size within each taxon can be set by a temperature-independent critical minimum value of mass-specific metabolic rate $q_{\min}$, a fall below which is not compatible with successful biological performance. 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 $q \geq q_{\min}$. 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. Here we test these predictions by analysing body lengths of the largest representatives of 24 poikilotherm taxa from the tropical, temperate and polar environments.

Investigation of maximum body sizes across diverse taxa and climatic zones requires extensive faunistic descriptions of the studied areas. We chose Great Britain and Colorado, USA as two well studied sites in the temperate zone and Wrangel Island (71°N, 179°W, Russia) as a representative polar territory (the whole island (22 257 km^2) is occupied by state nature reserve with relatively well studied fauna). As far as species lists for tropical countries are relatively fragmentary, we identified world's largest species in each of 24 taxa and determined their geographic ranges, to find that all of them inhabit tropical areas. For each region we calculated mean daily temperature T of the six warmest months presumably corresponding to maximum activity of poikilotherms. For the tropics, T was averaged over typical locations of the investigated species. For Wrangel Island, T was calculated as the mean for June, July and August, the only three months with mean temperature above 0°C. Temperature data were taken from Landsberg (1969–1984).

2. RESULTS AND DISCUSSION

Our analysis revealed that by linear body size, table 1, the largest tropical species of terrestrial poikilotherms exceed the largest representatives of the same taxa from Colorado, Great Britain and Wrangel Island by 2.3, 2.9 and 6.1 times, respectively. Body size change parallels the progressive decrease in mean ambient temperature: $T=26$°C

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Table 1. Maximum body size of terrestrial poikilotherms living at different ambient temperatures.
(L, largest linear body size in centimetres (body length unless otherwise stated) attained within a taxon in the studied area. Letters in brackets indicate continental locality of the largest tropical species: P, Philippines; H, St Helen Island; O, Oceania and Malaysia; A, Australia; S, South and Central America; Af, Africa. Sources for species descriptions are available from the authors upon request.)

	largest in the tropics		largest in Colorado		largest in Great Britain		largest on Wrangel Island	
taxon	species	L	species	L	species	L	species	L
springtails	*Paralobella orousetti* (P)	1.5			*Tomocerus longicornis*	0.6	*Isotoma gorodkovi*	0.3
earwigs	*Labidura herculeana* (H)	7.8	*Forficula auricularia*	2.3	*Forficula auricularia*	2.3		
orthopterans	*Macrolyristes imperator* (O)	12	*Microcentrum rhombifolium*	7.5	*Tettigonia viridissima*	5.5		
cockroaches	*Macropanesthia rhinoceros* (A)	7.5	*Periplaneta americana*	3.8	*Blatta orientalis*	2.5		
true bugs	*Lethocerus maximus* (S)	11	*Lethocerus americanus*	6.5	*Ranatra linearis*	3.0	*Chiloxanthus stellatus*	0.83
dragonflies[a]	*Petalura ingentissima* (A)	16	*Anax junius*	11	*Anax imperator*	10		
damselflies[a]	*Megaloprepus caerulatus* (S)	20			*Agrion vigro*	7.4		
butterflies[a]	*Ornithoptera alexandrae* (O)	25	*Papilio multicaudatus*	15	*Papilio machaon*	9.5	*Erebia fasciata*	6.0
moths[a]	*Thysania agrippina* (S)	28	*Ascalpha odorata*	15	*Acheronta atropos*	13	*Dicallomera kusnezovi*	4.5
long-horned beetles	*Titanus giganteus* (S)	17	*Ergates spiculates*	9			*Tetropium* sp.	1.8
scarabaeoid beetles	*Megasoma elephas* (S)	14	*Pseudolucanus mazama*	6	*Lucanus cervus*	7.5		
ground beetles	*Mormolyce phyllodes* (O)	7.8	*Pasimachus elongatus*	2.4	*Carabus intricatus*	3.6	*Carabus truncaticollis*	1.9
ants	*Camponotus gigas* (O)	3.1	*Camponotus herculeanus*	1.5	*Formica sanguinea*	1.2		
bees	*Megachile pluto* (O)	3.9	*Bombus pennsylvanicus*	2.4	*Bombus terrestris*	2.2	*Bombus hyperboreus*	2.2
spider wasps	*Pepsis heros* F. (S)	5.4	*Pepsis formosa*	4.5	*Priocnemis perturbator*	1.7		
short-horned flies	*Gauromydas heros* (S)	6.0	*Tabanus atratus*	5	*Tabanus sudeticus*	2.5		
spiders	*Theraphosa* sp. (S)	7.6	*Aphonopelma chalcodes*	5	*Dolomedes* sp.	2.4	*Alopecosa hirtipes*	1.25
mites, ticks	*Dinothrombium tinctorium* (Af)	1.6			*Trombidium holosericeum*	0.5		
earthworms[b]	*Rhinodrilus fafner* (S)	2.4			*Lumbricus terrestris*	1	*Eisenia nordenskioldii*	0.5
centipedes	*Scolopendra gigantea* (S)	30	*Scolopendra polymorpha*	11	*Haplophilus subterraneus*	7.0		
millipedes	*Archispirostreptus gigas* (Af)	28			*Cylindroiulus londinensis*	4.8		
land snails[c]	*Achatina achatina* (Af)	27			*Helix pomatia*	4.5		
snakes	*Python reticulatus* (O)	900	*Pituophis catenifer*	250	*Natrix natrix*	190		
lizards	*Varanus komodoensis* (O)	313	*Chemidophorus tesselatus*	39	*Anguis fragilis*	46		

[a] Wingspan.
[b] Body diameter.
[c] Shell length.

Table 2. Differences in maximum linear body sizes versus differences in environmental temperatures in terrestrial poikilotherms. (Notes: n is the number of taxa used in the comparison; R_{OB} is the observed ratio between body lengths of the largest representatives of the taxa considered in the compared territories, table 1; R_{TH} is the theoretical ratio predicted from equation (2.2) using $Q_{10}=2.3$ and the observed temperature difference ΔT between the compared territories; $\delta=((R_{\mathrm{TH}}-R_{\mathrm{OB}})/R_{\mathrm{TH}})\times 100\%$ is the relative difference between the observed and theoretically predicted values.)

			R_{OB}			
comparison	n	ΔT (°C)	range	mean ± 1 s.e.	R_{TH}	δ (%)
Tropics–Colorado	18	8	1.2–8.03	2.39 ± 0.37	2.10	−14
Tropics–Great Britain	23	12	1.6–6.8	3.23 ± 0.29	3.04	−6
Tropics–Wrangel Island	9	22	1.77–13.3	6.09 ± 1.13	7.66	+20
Colorado–Great Britain	17	4	0.67–2.65	1.42 ± 0.13	1.45	+2
Colorado–Wrangel Island	7	16	1.09–7.83	3.57 ± 0.89	4.40	+19
Great Britain–Wrangel Island	8	12	1.0–3.6	2.11 ± 0.28	3.04	+31

for the tropics, $T=18$°C for Colorado, $T=14$°C for Great Britain and $T=2$°C for Wrangel Island.

Within poikilothermic taxa mass-specific metabolic rate q grows with decreasing body size, but declines with decreasing temperature, $q \propto M^{-\alpha} Q_{10}^{(T_1-T_0)/(10^\circ\mathrm{C})}$, where M is body mass, T_0 is reference temperature, Q_{10} is typically 2–2.5 and α is typically in the vicinity of 1/4 or 1/3 (Peters 1983). At a given temperature the largest species feature minimum mass-specific metabolic rate $q_{\min}$. If $q_{\min}$ is universal for the taxon and independent of temperature, $q_{\min}=\mathrm{const}$, then for the largest species with body masses M_1 and M_2 living at temperatures T_1 and T_2 we have

$$M_1^{-\alpha} Q_{10}^{(T_1-T_0)/(10^\circ\mathrm{C})} = M_2^{-\alpha} Q_{10}^{(T_2-T_0)/(10^\circ\mathrm{C})}. \qquad (2.1)$$

Assuming that body shape is conserved within a given taxon, $L \propto M^{1/3}$, we obtain the following ratio for maximum linear body sizes L_1 and L_2 found at temperatures T_1 and T_2:

$$R_{\mathrm{TH}} \equiv L_1/L_2 = Q_{10}^{(\Delta T/10^\circ\mathrm{C})/3\alpha}, \qquad (2.2)$$

where $\Delta T \equiv T_1 - T_2$.

Theoretically predicted ratios R_{TH} calculated using mean representative values $Q_{10}=2.3$ and $\alpha=0.3$ for the temperature differences ΔT between the studied areas agree well with the observed mean ratios R_{OB}. For example, the largest terrestrial poikilotherms in Colorado are on average $R_{\mathrm{OB}}=1.42\pm0.13$ (s.e.) times longer than their counterparts in Great Britain (averaging is done over $n=17$ taxa studied in both Colorado and Great Britain, table 1). Temperature difference between Colorado and Great Britain is $\Delta T=4$°C, which gives $R_{\mathrm{TH}}=2.3^{0.4/(3\times0.3)}=1.45$. Relative difference $\delta=((R_{\mathrm{TH}}-R_{\mathrm{OB}})/R_{\mathrm{TH}})\times100\%$ between the theoretical and observed value is $\delta=+2\%$. Corresponding figures for comparison between the other geographic regions studied are given in table 2. The discrepancy between theoretical and observed values ranges from −14% to +31% and is larger for comparisons involving fewer taxa. For the three comparisons involving more than 15 taxa, the discrepancy between the observed and theoretical values ranges from −14% to +2%, table 2.

The obtained theoretical ratios R_{TH} between body lengths of the largest species of a given taxon living at different ambient temperatures can be independently tested by involving geographic regions different from those studied in the present paper. For example, the Antarctic Peninsula is situated at approximately the same latitude as Wrangel Island and features comparable temperatures. Hence, the prediction obtained for Wrangel Island that the largest polar species should be on average 7.7 times shorter in body length than the largest tropical species from the same taxon should apply to the Antarctic Peninsula as well. If, e.g. the largest tropical mite is about 16 mm in length, table 1, the largest mite on the Antarctic Peninsula should be able to reach about 2 mm in body length. This prediction is excellently confirmed by *Alaskozetes antarcticus*, the largest free-living mite on the Antarctic Peninsula (Block & Convey 1995).

The agreement between theory and data indicates that in the largest terrestrial poikilotherms from different climatic zones the expected decrease in metabolic rate caused by lower ambient temperature can be fully compensated by their smaller maximum body sizes. This suggests that the upper limit to body size within taxa can be set by a critical temperature-independent minimum of mass-specific metabolic rate $q_{\min}$, which prohibits attaining larger size at lower ambient temperatures (Singer *et al.* 1993; Seebacher *et al.* 1999; Makarieva *et al.* 2003).

Possible uniformity of $q_{\min}$ *across* different taxa, i.e. whether the largest representatives of different taxa in different climatic zones feature similar mass-specific metabolic rates, warrants investigation. Singer *et al.* (1993) found that mammals, independent of body size, do not tolerate a decrease of mass-specific metabolic rate below approximately 0.1 W kg^{-1}. It is interesting that the largest African centipede with measured metabolic rate (*Cormocephalus morsitans*, body mass 3.7 g, $T=20$°C) has a resting metabolic rate of approximately 0.3 W kg^{-1} (Klok *et al.* 2002), which coincides by the order of magnitude with the critical $q_{\min}$ value for mammals. For comparison, resting metabolic rate of males of the largest Antarctic tick *Ixodes uriae* (body mass 7 mg, $T=5$°C) is 0.22 W kg^{-1} (Lee & Baust 1982) while resting metabolic rate of one of the world's largest frogs, the African bullfrog *Pyxicephalus adspersus* (body mass 1 kg, $T=20$°C) is 0.14 W kg^{-1} (Loveridge & Withers 1981). These values for the largest representatives of taxa characterized by strikingly different body sizes and environmental temperatures are remarkably similar to each other and to the $q_{\min}$ value for mammals.

Oxygen concentration in the air is over an order of magnitude higher than that of water-dissolved oxygen. This means that per unit exerted drag force of the ventilatory muscles aquatic animals are unable to inhale as much oxygen as do air-breathing animals. Thus, even if at the microscopic scale the assimilation of oxygen by body cells of aquatic and terrestrial organisms is equally rapid (i.e. independent of the ambient oxygen concentration), metabolism of aquatic animals can be nevertheless limited by low oxygen concentrations in their environment due to the higher cost of delivering a unit oxygen mass into the organism via the body–environment interface. This can explain the difference in gigantism patterns between our study (larger poikilothermic giants at higher temperatures) and the study of benthic amphipods (Chapelle & Peck 1999), where largest body sizes were observed at lowest ambient temperatures associated with highest concentrations of dissolved oxygen. In terrestrial poikilotherms, the rate of oxygen uptake from the environment likely becomes a limiting factor during periods of maximum activity (e.g. flight), when metabolic rates in the regime of oxygen balance can exceed 500 W kg^{-1} and oxygen demand is very high (Harrison & Lighton 1998). (Note that the fact that such high rates have never been observed in oxygen-balanced aquatic animals unambiguously points to limitation of metabolic rate by low oxygen concentration in aquatic media.) Gigantism of extinct winged insects can be therefore related to atmospheric hyperoxia (Dudley 1998; Harrison & Lighton 1998). However, how elevated oxygen concentration translates into the observed gigantic insect sizes has not been theoretically quantified. Our study provides a quantitative tool for analysing higher ambient temperature as another factor possibly responsible for gigantism in extinct air-breathing poikilotherms. Under otherwise similar environmental conditions elevation of ambient temperature by 10°C could bring about a several-fold rise in maximum linear body size depending on the characteristic Q_{10} value for each taxon.

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