

LINEAR ALLOMETRIC RELATIONSHIP BETWEEN TOTAL METABOLIC ENERGY PER LIFE SPAN AND BODY MASS OF TERRESTRIAL MAMMALS IN CAPTIVITY

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Summary

Atanasov, A.T., 2006. Linear allometric relationship between total metabolic energy per life span and body mass of terrestrial mammals in captivity. *Bulg. J. Vet. Med.*, 9, No 3, 159–174.

The bioenergetic studies on animals have shown that basal metabolic rate P (kJ/d), is related to the body mass M (kg) of animals as expressed by the equation: $P = aM^k$, where a and k are allometric coefficients. The aim of this study was to investigate the allometric relationship between the total metabolic energy per life span $P_{ls} = PT_{ls}$, where T_{ls} is the life span, and the body mass of terrestrial mammals in captivity. Using statistical analyses it was shown that in 86 terrestrial mammals (Prototheria, Metatheria and Eutheria), a linear relationship between total metabolic energy per life span (PTIs, kJ) and body mass (M , kg) existed: $PT_{ls} = A_{ls}^+ M^{0.968}$, where T_{ls} (d) is the life span of animals in captivity in days, calculated from formula of Sacher $T_{ls}(y) = 11.8 \times M^{0.20}$ and the linear coefficient $A_{ls}^+ = 11.407 \times 10^5$ kJ/kg is the total metabolic energy, expended during the life span per 1 kg body mass of animals with physical dimension of “potential”. This linear coefficient can be regarded as relatively constant metabolic parameter for all terrestrial mammals, in spite of 6-degree differences between basal metabolic rate and body mass of animals. A mean values of linear coefficient \bar{A}_{ls} for 13 studied orders (Monotremata, Didelphimorphia, Dasyuromorphia, Peramelemorphia, Diprotodontia, Xenarthra, Pholidota, Rodentia, Lagomorpha, Artiodactyla, Carnivora, Chiroptera, Primates) grow from 5.6×10^5 kJ/kg in Didelphimorphia to 18.1×10^5 kJ/kg in Monkeys. It was shown that from the view of classical physics, the basal metabolic rate could be expressed as: $P = (A_{ls} a_{ch} M) / R_{ch}$, where A_{ls} – total metabolic energy per life span, per 1kg body mass, R_{ch} = body (volume/surface) ratio of organisms and $a_{ch} = R_{ch} / T_{ls}$ (m/s) – characteristics speed with values $5 \times 10^{-10} \div 2 \times 10^{-11}$ (m/s). The conventional ‘metabolic force’ $F_{met} = P / a_{ch} = (A_{ls} M) / R_{ch}$, related to basal metabolic rate P , was expressed as a function of metabolic potential (A_{ls}), body mass (M) and conventional length (R_{ch}), which is characteristics length for every organism.

Key words: force, gravitation, life span, mammals, metabolic energy

INTRODUCTION

The pattern existing between various fundamental characters of living organisms and their body size or mass are generally described as a power function called ‘allometric’. The bioenergetic studies on poikilothermic, mammals and aves (Hemmingsen, 1960; Kleiber, 1961; Hofman, 1983; Heusner, 1985; McNab,

1988; Gillooly *et al.*, 2001) have shown that the basal metabolic rate (P , kJ/d) is related to the body mass (M , kg) as expressed by the equation of the type $P = aM^k$. The biological meaning of linear and power coefficients a and k is connected with evolutionary range of animals (Zotin & Lamprecht, 1996; Atana-

sov & Dimitrov, 2002). In previous works Atanasov (2005a, b, c) using life span (longevity) (T_{ls} , d) of animals as a parameter, showed that the relationships between the total metabolic energy per life span ($P_{ls}=PT_{ls}$) and the body mass (M) in a great number of animals (poikilothermic, mammals and birds) was expressed by the linear equation of the type $P_{ls}=A_{ls}M$, where A_{ls} is the total metabolic energy per life span, per 1 kg body mass (with a physical SI dimension as the chemical and the gravitational potentials, i.e. kJ/kg). A_{ls} for multicellular poikilothermic organisms range from 1×10^5 kJ/kg in snakes to about 5×10^5 kJ/kg in fish and reptiles (Atanasov, 2005b).

A prognostic estimation of A_{ls} in mammals can be made from the law of Kleiber for the basal metabolic rate (Kleiber, 1961): $P=70M^{0.75}$ (P , kcal/d; M , kg) and the formula of Sacher (1959) for the longevity of mammals in captivity: $T_{ls}=11.8M^{0.20}$ (T_{ls} , years; M , kg). From the relation $A_{ls}=(PT_{ls})/M$, we can calculate the total metabolic energy per life span, utilized per 1kg body mass as a function of mass: $A_{ls}=(12.6 \times 10^5) M^{-0.05}$, kJ/kg. This formula shows, that A_{ls} slightly depends on body mass of mammals ($\sim M^{-0.05}$). Indeed, for animals with difference in body mass one million (from 1 g to 1×10^3 kg), the computed values of A_{ls} change only two-fold: from 8.9×10^5 kJ/kg (for animals with body mass ~ 1 g) to 19.8×10^5 kJ/kg (for animals with body mass $\sim 1 \times 10^3$ kg).

The aim of this study was to establish and calculate the exact allometric relationship between the total metabolic energy per life span and the body mass in a wide range of terrestrial mammals in captivity, with variation of the rate of metabolism and the body mass of about 6 orders of magnitude.

DATA AND METHODS

Data for the basal metabolic rate (P), body mass (M) and life span (T_{ls}) for 86 terrestrial species, including 3 monotremes (subclass Prototheria), 16 marsupials (subclass Theria, infraclass Metatheria) and 67 "placentals" (subclass Theria, Infraclass Eutheria) are presented in Table 1.

Data for the basal metabolic rate and the body mass of animals in orders were obtained from scientific literature (Table 1).

The life span of mammals in captivity (T_{ls}) was calculated from the formula of Sacher (1959): $T_{ls}(\text{years})=11.8 M^{0.20}$, where M is in kg. Only for monkeys we used the data of Cutler (1984) for maximum life span in captivity.

For each animal, the total metabolic energy per life span (PT_{ls} , kJ) was calculated as a product of the basal metabolic rate (P , kJ/d) and the life span (T_{ls} , d).

The total metabolic energy per life span, per 1 kg body mass (A_{ls}) was calculated as a ratio of PT_{ls} (kJ) and M (kg) of mammals: $A_{ls}=(PT_{ls})/M$ (kJ/kg).

A statistic package "Statistica" of the Institute for Space Research (Bulgarian Academy of Sciences) was used for statistical calculations.

RESULTS

The studied mammalian species, the body mass, the basal metabolic rate, the life span in captivity, the calculated data for the total metabolic energy per life span (PT_{ls}), and the total metabolic energy per life span, per 1 kg body mass (PT_{ls}/M) are given in Table 1.

The logarithmic graphic of the relationship between PT_{ls} and M of terrestrial mammals is presented on Fig. 1.

Table 1. Data for the body mass (M), basal metabolic rate (P), life span (T_{ls}), total metabolic energy per life span (PT_{ls}) and the total metabolic energy per life span per 1 kg body mass (A_{ls}) for 86 terrestrial mammals in captivity

Mammals	M (kg)	P (kJ/day)	T _{ls} (years)	PT _{ls} (kJ)	A _{ls} (kJ/kg)	Reference No*
Subclass PROTOTHERIA						
Order Monotremata						
1. Echidna (<i>Tachiglossus aculeatus</i>)	2.5	301.5	14.17	15.59×10 ⁵	6.236×10 ⁵	27, 34
2. Platypus (<i>Ornithorhynchus anatinus</i>)	1.3	228.6	12.43	10.37×10 ⁵	7.97×10 ⁵	12, 34
3. Long-beaked echidna (<i>Zaglossus bruijii</i>)	10.3	593.78	18.8	40.745×10 ⁵	3.956×10 ⁵	27, 34
Subclass THERIA, Infraclass METATHERIA						
Order Didelphimorphia						
4. Opossum (<i>Lutreolina crassicaudata</i>)	0.812	195.85	11.3	8.077×10 ⁵	9.947×10 ⁵	24, 31, 34
5. South American opossum (<i>Didelphis marsupialis</i>)	1.329	298.66	12.5	13.63×10 ⁵	10.25×10 ⁵	24, 31, 34
6. Virginia opossum (<i>Didelphis virginiana</i>)	3.257	518.5	14.9	28.19×10 ⁵	8.655×10 ⁵	28, 34
Order Dasyuromorphia						
7. Fat-tailed false antechinus (<i>Antechinus macdonnellensis</i>)	14.1×10 ⁻³	9	5.03	16.5×10 ³	11.7×10 ⁵	22, 34
8. Brown antechinus (<i>Antechinus stuartii</i>)	36.5×10 ⁻³	17.6	6.08	39×10 ³	10.68×10 ⁵	9, 31, 34
9. Kultarr (<i>Antechinomus laniger</i>)	8.5×10 ⁻³	5.166	4.55	8.58×10 ³	10.1×10 ⁵	22, 34
10. Kowari (brush-tailed marsupial rat) (<i>Dasyuroides byrnei</i>)	89×10 ⁻³	37.35	7.27	99.1×10 ³	11.13×10 ⁵	22, 34

Table 1 (continued)

Mammals	M (kg)	P (kJ/day)	T _{ls} (years)	PT _{ls} (kJ)	A _{ls} (kJ/kg)	Reference No*
11. Fat-tailed dunnart (<i>Sminthopsis crassicaudata</i>)	15×10 ⁻³	9.64	5.09	17.9×10 ³	11.93×10 ⁵	28, 31, 34
12. Pigmy planigale (<i>Planigale maculata</i>)	13×10 ⁻³	13.65	4.95	24.66×10 ³	18.97×10 ⁵	30, 34
13. Tasmanian devil (<i>Sarcophilus harrisi</i>)	5.05	628.11	16.3	37.37×10 ⁵	7.4×10 ⁵	32, 34
Order Peramelemorphia						
14. Brown bandicoot (<i>Isodon macrourus</i>)	1	200.9	11.8	8.65×10 ⁵	8.65×10 ⁵	15, 31, 34
15. Long-nosed bandicoot (<i>Perameles nasuta</i>)	0.645	152.46	10.81	6.01×10 ⁵	9.317×10 ⁵	15, 31, 34
Order Diprotodontia						
16. Brushtail possum (<i>Trichosurus vulpecula</i>)	1.982	305.5	13.5	15.05×10 ⁵	7.59×10 ⁵	9, 31, 34
17. Kangaroo (<i>Macropus robustus</i>)	4.69	693.9	16.07	40.7×10 ⁵	8.67×10 ⁵	33, 34
18. Red kangaroo (<i>Macropus rufus</i>)	40	4.10 ³	24.67	36×10 ⁶	9×10 ⁵	33, 34
19. Tamar wallaby (<i>Macropus eugenii</i>)	4.796	671	16.5	39.55×10 ⁵	8.246×10 ⁵	9, 31, 34
Subclass THERIA, Infraclass EUTHERIA						
Order Xenarthra						
20. Three-toed sloth (<i>Bradypus variegatus</i>)	3.79	331	15.4	18.6×10 ⁵	4.9×10 ⁵	25, 34
21. Nine-banded armadillo (<i>Dasybus novemcinctus</i>)	3.32	384.4	15	21×10 ⁵	6.325×10 ⁵	26, 34

Table 1 (continued)

Mammals	M (kg)	P (kJ/day)	T _{is} (years)	PT _{is} (kJ)	A _{is} (kJ/kg)	Reference No*
Order Pholidota						
22. Pangolin (<i>Manis tricuspis</i>)	2.73	439.7	14.4	23.11×10 ⁵	8.465×10 ⁵	13, 31, 34
23. Scaly anteater (<i>Manis javanica</i>)	4.22	529.3	15.7	30.33×10 ⁵	7.19×10 ⁵	27, 34
Order Rodentia						
24. Hamster (<i>Cricetus cricetus</i>)	0.362	111.75	9.63	3.93×10 ⁵	10.85×10 ⁵	11, 31, 34
25. Spiny pocket mouse (<i>Liomys salvini</i>)	43.8×10 ⁻³	22.51	6.3	51.76×10 ³	11.8×10 ⁵	14, 34
26. Mexican mouse (<i>Liomys irroratus</i>)	48.1×10 ⁻³	25.99	6.43	61×10 ³	12.68×10 ⁵	14, 34
27. Harvest mouse (<i>Micromys minutus</i>)	9.8×10 ⁻³	17.97	4.68	30.7×10 ³	31.3×10 ⁵	28, 31, 34
28. Mexican vole (<i>Microtus mexicanus</i>)	28×10 ⁻³	22	5.77	46.3×10 ³	16.5×10 ⁵	28, 31, 34
29. Golden mouse (<i>Ochrotomys nuttalli</i>)	19.5×10 ⁻³	23.78	5.37	46.61×10 ³	23.9×10 ⁵	18, 31, 34
30. House mouse (<i>Mus musculus</i>)	0.021	20.9	5.45	41.57×10 ⁴	19.8×10 ⁵	28, 34
31. Brushy-tailed woodrat (<i>Neotoma citerea</i>)	0.321	120.78	9.4	4.14×10 ⁵	12.9×10 ⁵	2, 34
32. Desert woodrat (<i>Neotoma lepida</i>)	0.139	48.24	7.95	14×10 ⁴	10×10 ⁵	19, 31, 34
33. Dusky-footed woodrat (<i>Neotoma fuscipes</i>)	0.187	71.27	8.44	21.95×10 ⁴	11.7×10 ⁵	9, 31, 34

Table 1 (continued)

Mammals	M (kg)	P (kJ/day)	T _{ls} (years)	PT _{ls} (kJ)	A _{ls} (kJ/kg)	Reference No*
34. White-throated woodrat (<i>Neotoma albigula</i>)	0.172	61.4	8.3	18.6×10 ⁴	10.8×10 ⁵	2, 34
35. Musk rat (<i>Ondatra zibethicus</i>)	0.842	333	11.4	13.86×10 ⁵	16.45×10 ⁵	34, 36
36. Pocket mouse (<i>Perognathus longimembris</i>)	11.5×10 ⁻³	11.428	4.8	20×10 ³	17.39×10 ⁵	4, 31, 34
37. Hispid pocket mouse (<i>Perognathus hispidus</i>)	39.5×10 ⁻³	23.82	6.18	53.73×10 ³	13.6×10 ⁵	34, 37
38. Cactus mouse (<i>Peromyscus eremicus</i>)	21.5×10 ⁻³	15.35	5.47	30.65×10 ³	14.25×10 ⁵	29, 34
39. California mouse (<i>Peromyscus californicus</i>)	45.5×10 ⁻³	22.61	6.36	52.49×10 ³	11.53×10 ⁵	29, 34
40. White-footed mouse (<i>Peromyscus leucopus</i>)	22.2×10 ⁻³	26.77	5.5	53.74×10 ³	24.2×10 ⁵	28, 31, 34
41. Chinchilla (<i>Chinchilla laniger</i>)	0.494	111.99	10.2	4.17×10 ⁵	8.44×10 ⁵	17, 34
42. Plains viscacha (<i>Lagostomus maximus</i>)	6.784	916.36	17.3	57.86×10 ⁵	8.53×10 ⁵	17, 34
43. Rock cavy (<i>Kerodon rupestris</i>)	0.750	193	11.1	7.82×10 ⁵	10.42×10 ⁵	28, 31, 34
44. Guinea pig (<i>Cavia porcellus</i>)	0.5	192	10.27	7.2×10 ⁵	14.4×10 ⁵	28, 34
45. Woodchuck (<i>Marmota monax</i>)	2.65	319.6	14.3	16.68×10 ⁵	6.29×10 ⁵	28, 34
46. Bush rat (<i>Rattus fuscipes</i>)	0.076	40.68	7	1.04×10 ⁵	13.67×10 ⁵	5, 31, 34

Table 1 (continued)

Mammals	M (kg)	P (kJ/day)	T _{is} (years)	PT _{is} (kJ)	A _{is} (kJ/kg)	Reference No*
47. Swamp rat (<i>Rattus lutreolus</i>)	0.109	30.49	7.6	8.46×10 ⁴	7.76×10 ⁵	6, 31, 34
48. Black rat (<i>Rattus rattus</i>)	0.132	80.86	7.87	2.32×10 ⁵	17.57×10 ⁵	7, 31, 34
49. Dusky field rat (<i>Rattus sordidus</i>)	0.187	51.4	8.4	15.76×10 ⁴	8.43×10 ⁵	7, 31, 34
50. Hispid cotton rat (<i>Sigmodon hispidus</i>)	0.161	168.4	8.18	5.028×10 ⁵	31.23×10 ⁵	28, 34
Order Lagomorpha						
51. Brown hare (<i>Lepus europaeus</i>)	2.5	528	14.17	23.31×10 ⁵	10.92×10 ⁵	28, 34
52. Snowshoe hare (<i>Lepus americanus</i>)	1.581	686.4	12.93	32.4×10 ⁵	20.48×10 ⁵	28, 34
53. Blacktailed jackrabbit (<i>Lepus californicus</i>)	2.3	632.3	13.9	31.62×10 ⁵	13.75×10 ⁵	28, 34
54. Mountain hare (<i>Lepus timidus</i>)	3.004	521.6	14.7	27.99×10 ⁵	9.316×10 ⁵	28, 34
55. Jackrabbit (<i>Lepus alleni</i>)	3.362	729.8	15	39.95×10 ⁵	11.88×10 ⁵	28, 34
56. Cottontail (<i>Sulvilagus audubonii</i>)	0.702	220.12	11	8.84×10 ⁵	12.6×10 ⁵	28, 34
Order Artiodactyla						
57. Pronghorn (<i>Antilocapra americana</i>)	32	4322	23.6	37.23×10 ⁶	11.6×10 ⁵	28, 34
58. Dromedarian camel (<i>Camelus dromedarius</i>)	407	23630	39.2	338×10 ⁶	8.3×10 ⁵	31, 34, 35
59. Asian elephant (<i>Elephas maximus</i>)	3×10 ³	165×10 ³	58.5	35.23×10 ⁸	11.7×10 ⁵	31, 34, 35

Table 1 (continued)

Mammals	M (kg)	P (kJ/day)	T _h (years)	PT _h (kJ)	A _h (kJ/kg)	Reference No*
60. Roe deer (<i>Capreolus capreolus</i>)	19	3666	21.2	283.67×10 ⁵	14.9×10 ⁵	34, 38
61. Red deer (<i>Cervus elaphus</i>)	58	7.8×10 ³	26.6	75.73×10 ⁶	13×10 ⁵	1, 31, 34
62. Horse (<i>Equus caballus</i>)	400	32000	39	4.555×10 ⁸	11.38×10 ⁵	34, 35
63. Mouflon (<i>Ovis aries</i>)	49	4200	25.7	39.4×10 ⁶	8.04×10 ⁵	28, 34
64. Bighorn sheep (<i>Ovis canadensis</i>)	65	10660	27	105×10 ⁶	16.15×10 ⁵	3, 34
65. African buffalo (<i>Bubalus caffer</i>)	420	29400	39.5	423.87×10 ⁶	10.1×10 ⁵	28, 34
66. Wild goat (<i>Rupicapra rupicapra</i>)	40	3140	24.6	282×10 ⁵	7.05×10 ⁵	28, 34
67. Feral pig (<i>Sus scrofa</i>)	140	12×10 ³	31.7	138.8×10 ⁶	9.91×10 ⁵	34, 35
68. Collared peccary (<i>Tayassu tajacu</i>)	20.2	2826	21.5	22.18×10 ⁶	10.98×10 ⁵	31, 34, 39
Order Carnivora						
69. Wolverine (<i>Gulo gulo</i>)	12.7	2818	19.6	201.6×10 ⁵	15.87×10 ⁵	16, 31, 34
70. Badger (<i>Meles meles</i>)	11.05	1439.2	19	99.8×10 ⁵	9.03×10 ⁵	16, 31, 34
71. Fox (<i>Vulpes vulpes</i>)	5.01	1208.4	16.3	71.9×10 ⁵	14.35×10 ⁵	28, 34
72. Coyote (<i>Canis latrans</i>)	10	1320.5	18.7	90.13×10 ⁵	9×10 ⁵	28, 34
73. Domestic dog (<i>Canis familiaris</i>)	14	1881	20	137.3×10 ⁵	9.807×10 ⁵	31, 34, 35
74. Jaguar (<i>Panthera onca</i>)	18	2436	21	186.7×10 ⁵	10.37×10 ⁵	28, 34
75. Wildcat (<i>Felis silvestris</i>)	3	546	14.7	29.3×10 ⁵	9.76×10 ⁵	28, 34, 35
76. Mink (<i>Mustela vison</i>)	0.660	238.6	10.86	9.46×10 ⁵	14.33×10 ⁵	10, 34

Table 1 (continued)

Mammals	M (kg)	P (kJ/day)	T _{is} (years)	PT _{is} (kJ)	A _{is} (kJ/kg)	Reference No*
Order Chiroptera						
77. Vampire bat (<i>Desmodus rotundus</i>)	0.029	9.65	5.8	20.43×10 ³	7.045×10 ⁵	23, 31, 34
78. White-lined bat (<i>Vampyrops lineatus</i>)	0.022	15.6	5.5	31.31×10 ³	14.23×10 ⁵	23, 31, 34
79. Western Mastiff bat (<i>Eumops perotis</i>)	0.057	14.2	6.65	34.46×10 ³	6.04×10 ⁵	20, 34
80. Ghost bat (<i>Macroderma gigas</i>)	0.148	67.97	8.05	199.7×10 ³	13.5×10 ⁵	21, 34
81. Grey-headed flying fox (<i>Pteropus poliocephalus</i>)	0.598	153	10.6	5.92×10 ⁵	9.899×10 ⁵	28, 34
Order Primates (Monkeys)						
82. Chimpanzee (<i>Pan troglodytes</i>)	45	4.62×10 ³	40	67.45×10 ⁶	15×10 ⁵	8, 31, 34
83. Rhesus macaque (<i>Macaca mulatta</i>)	5	960	26	91.1×10 ⁵	18.22×10 ⁵	8, 31, 34
84. Orangutan (<i>Pongo pygmaeus</i>)	150	15.54×10 ³	50	283.6×10 ⁶	18.9×10 ⁵	8, 31, 34
85. Gorilla (<i>Gorilla gorilla</i>)	250	21×10 ³	60	460×10 ⁶	18.4×10 ⁵	8, 31, 34
86. Gibbon (<i>Hylobates lar</i>)	8	1512	29	160×10 ⁵	20×10 ⁵	8, 31, 34

*Literature sources: 1. Brockway & Maloily (1968); 2. Brown (1968); 3. Chappel & Hudson (1978); 4. Chew *et al.* (1967); 5. Collins (1973a); 6. Collins (1973b); 7. Collins & Bradshaw (1973); 8. Cutler (1984); 9. Dawson & Hulbert (1970); 10. Farrell & Wood (1968); 11. Gorecki & Wolek (1975); 12. Grant & Dawson (1978); 13. Hildwein (1972); 14. Hudson & Rummel (1966); 15. Hulbert & Dawson (1974); 16. Iversen (1972); 17. Kohl (1980); 18. Layne & Dolan (1975); 19. Lee (1963); 20. Leimer (1966); 21. Leimer & Nelson (1967); 22. MacMillen & Nelson (1969); 23. McNab (1969); 24. McNab (1978a); 25. McNab (1978b); 26. McNab (1980); 27. McNab (1984); 28. McNab (1988); 29. McNab & Morrison (1963); 30. Morton & Lee (1978); 31. Naumov & Kuzaykina (1971); 32. Nicol & Maskrey (1980); 33. Prosser (1977); 34. Sacher (1959); 35. Schmidt-Nielsen (1984); 36. Sherer & Wunder (1979); 37. Wang & Hudson (1970); 38. Weiner (1977); 39. Zervanos (1975).

Statistical analyses of data showed that there was a linear relationship between the total metabolic energy per life span in captivity and the body mass of terrestrial animals:

$$\log (PT_{ls}) = 6.0572 + 0.968 \log M \quad (1)$$

with $R^2 = 0.98$

If $\log A_{ls}^+ = 6.0572$, the above equation can be presented as:

$$\log (PT_{ls}) = \log (A_{ls}^+ M^{0.968}) \quad (2)$$

where A_{ls}^+ is the total metabolic energy spent during the life span per 1 kg body mass of animal with the physical dimension of “potential”, and further:

$$PT_{ls} = A_{ls}^+ M^{0.968} \quad (3)$$

with linear coefficient $A_{ls}^+ = 11.407 \times 10^5$ kJ/kg.

The correlation coefficient (R^2) between PT_{ls} and M was 0.98. This means that relationship between PT_{ls} and M is not random and $A_{ls}^+ = 11.407 \times 10^5$ kJ/kg

was a constant or parameter for all 13 studied terrestrial orders. The individual values of A_{ls} for all 86 species are given in Table 1.

The mean values of allometric coefficients ($\bar{A}_{ls} \pm S_A$) for the different orders given in Table 1 are: for order Monotremata (6.054 ± 1.16) $\times 10^5$ kJ/kg, $n=3$; order Didelphimorphia (9.62 ± 0.49) $\times 10^5$ kJ/kg, $n=3$; order Dasyuromorphia (14.3 ± 1.098) $\times 10^5$ kJ/kg, $n=7$; order Paramelemorphia (9 ± 0.32) $\times 10^5$ kJ/kg, $n=2$; order Diprotodontia (8.376 ± 0.304) $\times 10^5$ kJ/kg, $n=4$; order Xenarthra (5.6 ± 0.712) $\times 10^5$ kJ/kg, $n=2$; order Pholidota (7.8 ± 0.638) $\times 10^5$ kJ/kg, $n=2$; order Rodentia (14.67 ± 1.27) $\times 10^5$ kJ/kg, $n=27$; order Lagomorpha (11.5 ± 1.75) $\times 10^5$ kJ/kg, $n=6$; order Artiodactyla (11.1 ± 0.78) $\times 10^5$ kJ/kg, $n=12$; order Carnivora (16.875 ± 1.79) $\times 10^5$ kJ/kg, $n=8$; order Chiroptera (10.14 ± 1.65) $\times 10^5$ kJ/kg, $n=5$; order Pri-

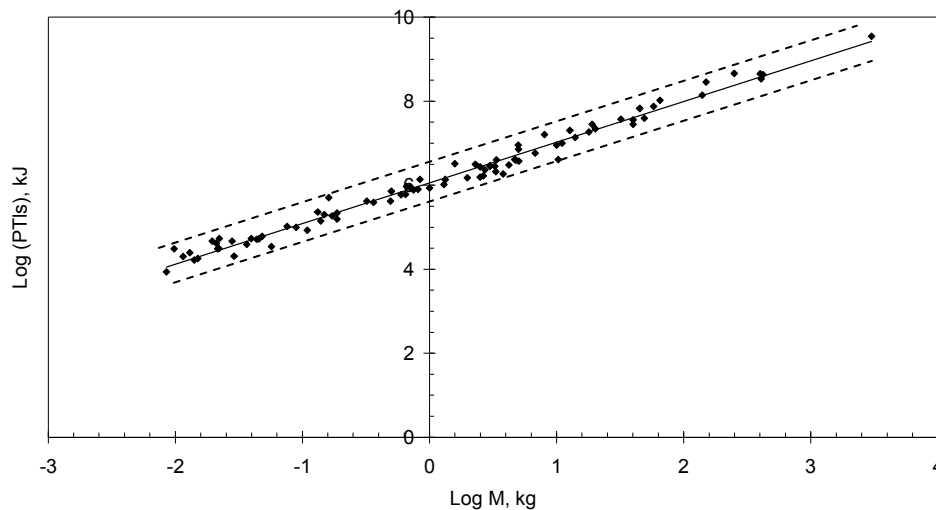


Fig. 1. Relationship between the total metabolic energy per life span (PT_{ls} , kJ) and the body mass (M , kg) for 86 terrestrial mammals (in captivity), including 3 monotremes (Prototheria), 16 marsupials (Metatheria) and 67 “placentals” (Eutheria). The 95% confidence limits are shown by dashed lines.

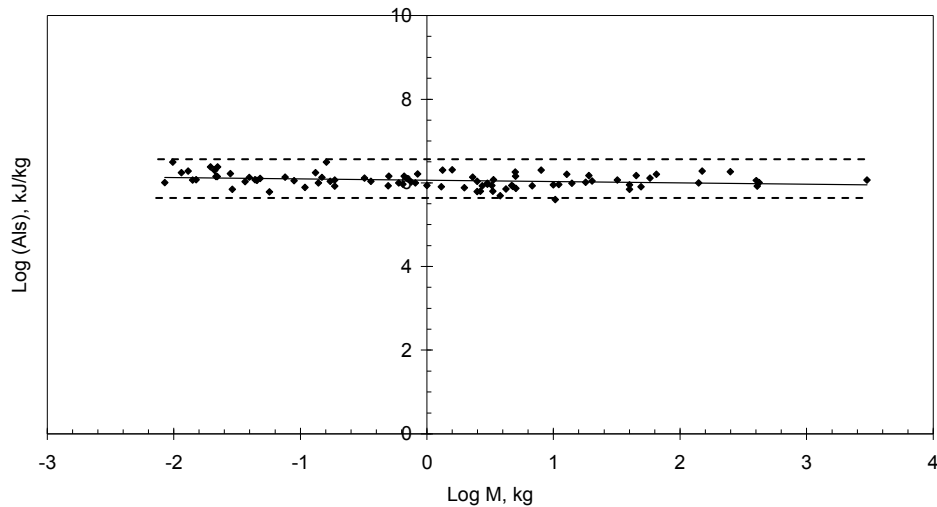


Fig. 2. Relationship between the total metabolic energy per life span per unit body mass ($A_{Is}=PT_{Is}/M$ kJ/kg) and the body mass (M , kg) for 86 terrestrial mammals in captivity (Prototheria, Metatheria and Eutheria). The 95% confidence limits are shown by dashed lines.

mates $(18.1 \pm 0.835) \times 10^5$ kJ/kg, $n=5$.

The mean \bar{A}_{Is} value for all 13 orders is 11.8 kJ/kg, which is near to A_{Is}^+ of 11.407×10^5 kJ/kg (since \bar{A}_{Is} and A_{Is}^+ have one and same mathematical meaning).

DISCUSSION

The study shows that 1 kg body mass of terrestrial mammals from any subclasses and orders expends nearly an equal amount of metabolic energy $(5.6 \div 18.1) \times 10^5$ kJ/kg, during the life. Exhaustion of this energy possibly leads to biological death of the animals. Our survey shows that the body mass, basal metabolic rate and the life span of animals are three mutually related parameters, so that the ratio $A_{Is}=(PT_{Is})/M$ remains a relatively constant parameter. \bar{A}_{Is} for the 13 orders differs 3.5-fold (from 5.6×10^5 to 18.1×10^5 kJ/kg), in spite of the $\sim 10^6$ fold differences between basal metabolic rate

and body mass of animals. For example: the body mass of studied mammals varied from minimum value 8.5×10^{-3} kg in the marsupial *Antechinomus laniger* to a maximum value 3×10^3 kg in the elephant. The amount of spent total metabolic energy per life span (PT_{Is}) varies from 8.58×10^3 kJ in *Antechinomus laniger* to 32.52×10^8 kJ in the elephant. Despite of the considerable differences in the basal metabolic rate and the body mass of *Antechinomus laniger* and the elephant, the individual values of A_{Is} for the two animals are nearly equal to 10.1×10^5 kJ/kg and 10.8×10^5 kJ/kg respectively.

The highest values of $A_{Is}=(15 \div 20) \times 10^5$ kJ/kg were those of the species from order Primates (monkeys).

The graphical relationship between individual values of A_{Is} and the body mass for 86 terrestrial species is given on Fig. 2. The statistical calculation showed that:

$$A_{Is} = 11.407 \times 10^5 M^{-0.0319} \text{ kJ/kg} \quad (4)$$

This relation is very near to the theoretical relation $A_{ls} = 12.6 \times 10^5 M^{-0.05}$ kJ/kg, calculated by us in Introduction. But in this case, the dependence between A_{ls} and M is much weaker, since the power coefficient is 0.0319.

The existence of linear relationship between the total metabolic energy per life span and body mass of mammals leads to some consequences:

First, in a fixed steady state values of basal metabolic rate, the duration of life is a time interval, for which the total metabolic energy per life span becomes directly proportional to the body mass of animals.

From the relation (3): $PT_{ls} = A_{ls}M$ we obtained a new equation for the basal metabolic rate: $P = (A_{ls}M)/T_{ls}$, that was related to the body mass (M), life span (T_{ls}) and the linear coefficient (A_{ls}) in comparison to power relation $P = aM^k$, that was related to the body mass (M), the linear coefficient (a), and the power coefficient (k).

Second, from the relation (3) we obtained the inversely proportional relation between the life span (T_{ls} , days) and the basal metabolic rate, per 1kg body mass (intensity of the metabolism) $P^* = P/M$ (kJ/d.kg):

$$T_{ls} = A_{ls} / P^* \quad (5)$$

For order Primates (monkeys) the same relation, with mean value of coefficient $\bar{A}_{ls} = 18.1 \times 10^5$ kJ/kg can be modified to: $T_{ls} = (18.1 \times 10^5) / P^*$. For example, in the Tarsier monkey with life span $T_{ls} \approx 10$ years (3650 d) we obtained an intensity of metabolism $P^* = 496$ kJ/d.kg. This calculated value for P^* is close to the experimental value 518 kJ/kg.d for this monkey, measured by Cutler (1984).

Third, the size of living organisms varies from 10^{-6} m to ~ 10 m and the life span from 10^3 s to ~ 100 years. This

shows, that living organisms are into the field of classical physics with respect to their size and life span. According to the concept of classical physics, the basal metabolic rate is the work (or energy), spent from living organism per unit time i.e. the basal metabolic rate have the dimension of 'power':

$$P_{met} (J/s) = \text{Work/Time} = \text{Power} = (\text{Force} \times \text{Displacement})/\text{Time or}$$

$$P_{met} (J/s) = P_{ls}/T_{ls} = (F \times R_{ch})/T_{ls},$$

where F is the force, $R_{ch} = V/S$ (volume/surface) ratio of the living organism.

According to the classical mechanics, the total metabolic energy per life span (P_{ls} , kJ) can be expressed as a product of the "power" (P_{met} , kJ/s) and the life span (T_{ls} , s) or as a product of conventional "metabolic force" (F_{met} , N) and given conventional 'displacement' equal to characteristics length (R_{ch} , m): $P_{ls} = P_{met} \times T_{ls} = F_{met} \times R_{ch}$. Since the basal metabolic rate is connected with body volume/surface ratio (Metzler, 1980), the characteristic length can be presented as: $R_{ch} = V/S$ (m), where V is the body volume, S is the body surface of organism. From the relationship: $P_{met} \times T_{ls} = F_{met} \times R_{ch} = A_{ls} \times M$, the conventional "metabolic force" acting across body mass (volume) of organism was:

$$F_{met} = (A_{ls} \times M) / R_{ch}, (N) \quad (6)$$

The basal metabolic rate expressed through conventional "metabolic force" was $P_{met} = (F_{met} \times R_{ch}) / T_{ls} = F_{met} \times a_{ch}$, where $a_{ch} = R_{ch} / T_{ls}$ is the characteristics speed. The calculation for the characteristics speed a_{ch} shows, that the characteristics speed has relatively constant values for living organisms in the interval $5 \times 10^{-10} \div 2 \times 10^{-11}$ m/s (Atanasov, 2006). For the basal metabolic rate as a function of R_{ch} we found:

$$P_{\text{met}} = F_{\text{ls}} \times a_{\text{ch}} = (A_{\text{ls}} \times a_{\text{ch}} \times M) / R_{\text{ch}} \text{ (J/s)} \quad (7)$$

The conventional “metabolic force” F_{met} and the gravitation force F_{g} acting on body mass M (in the gravitation field of the Earth) could be compared:

1. The gravitation force is expressed as: $F_{\text{g}} = M \times g$, where $g = 9.8 \text{ m/s}^2$ is the acceleration of a body on the surface of the Earth.

2. The conventional “metabolic force” is expressed as: $F_{\text{met}} = (A_{\text{ls}} \times M) / R_{\text{ch}}$, where A_{ls} is the total metabolic energy per life span (per 1 kg body mass) playing role of “metabolic potential”. M is the body mass of living organism and R_{ch} is the characteristic (volume/surface) ratio of organism, which in this case play role of conventional “displacement”.

3. The basal metabolic rate (power of metabolism) is expressed as:

$$P_{\text{met}} = (A_{\text{ls}} \times a_{\text{ch}} \times M) / R_{\text{ch}},$$

where A_{ls} corresponds to the “metabolic potential” of living organism, a_{ch} is the characteristic speed $\approx 5 \times 10^{-10} \div 2 \times 10^{-11} \text{ m/s}$, M is the body mass and R_{ch} is the characteristic (volume/surface) ratio of living organism.

For bacteria with body mass $M = 1.10^{-15} \text{ kg}$, $R_{\text{ch}} = 0.083 \times 10^{-6} \text{ m}$ (Metzler, 1980), $A_{\text{ls}} = 0.1 \times 10^8 \text{ J/kg}$ (Atanasov, 2005b) for $T_{\text{ls}} = 20 \text{ min}$, the calculated metabolic force is: $F_{\text{met}} = 0.12 \text{ N}$ and the calculated gravitation force is: $F_{\text{g}} = M \times g \approx 1.10^{-14} \text{ N}$. The ratio of the two forces is $F_{\text{met}} / F_{\text{g}} = 1.2 \times 10^{13}$.

For a mouse with body mass $M = 0.021 \text{ kg}$, $R_{\text{ch}} = 2.7 \times 10^{-3} \text{ m}$ (Metzler, 1980), $A_{\text{ls}} = 5.42 \times 10^8 \text{ J/kg}$ for $T_{\text{ls}} = 1.5 \text{ years}$ (Atanasov, 2005a), the calculated metabolic force is $F_{\text{met}} = 4.2 \times 10^9 \text{ N}$, and the calculated gravitation force is: $F_{\text{g}} = M \times g = 0.2 \text{ N}$. The ratio of the two forces is: $F_{\text{met}} / F_{\text{g}} = 2.1 \times 10^{10}$.

For a man with body mass $M = 90 \text{ kg}$,

$R_{\text{ch}} = 3.3 \times 10^{-2} \text{ m}$ (Metzler, 1980), $A_{\text{ls}} = 30 \times 10^8 \text{ J/kg}$ for $T_{\text{ls}} = 70 \text{ years}$ (Atanasov, 2005a) the calculated metabolic force is $F_{\text{met}} = 8.1 \times 10^{12} \text{ N}$, and the calculated gravitation force is: $F_{\text{g}} = M \times g = 882 \text{ N}$. The ratio of the two forces is $F_{\text{met}} / F_{\text{g}} = 9.2 \times 10^9$.

Therefore, we can say that the comparison between the “metabolic force” and the gravitational force is possible, because the total metabolic energy per life span is linearly proportional to the body mass of living organisms. Possibly, the linear relationship between the total metabolic energy per life span and the body mass of animals appears a general allometric law in animal energetic, since it is valid for poikilotherms, mammals and aves (Atanasov, 2005a, b, c).

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Paper received 19.09.2005; accepted for publication 04.07.2006

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