



*Original Contribution*

**ALLOMETRIC SCALING OF TOTAL METABOLIC ENERGY PER LIFESPAN IN LIVING ORGANISMS**

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**ABSTRACT**

The purpose of the study is to establish and calculate the relationship between the total metabolic energy per lifespan and the body mass of Ectotherms, Mammals and Aves ( $n=278$  living organisms) with 21 orders of magnitude variation between their body mass- from Bacteria to *Elephas maximum* and *Struthio camelus*.

The study shows the existence of a linear relationship between the total metabolic energy per lifespan  $P_{ls}$  (kJ), and the body mass  $M$  (kg) of all species from type:  $P_{ls}=A_{ls}M^{1.0787\pm 0.11}$  with  $R^2=0.980$ , coefficient  $A_{ls}=15.18\times 10^5$  kJ/kg, standard error of the exponent  $SE=\pm 0.11$  and 95% confidence interval of the exponent (0.968 - 1.188). The same relationship for Ectotherms, Mammals and Aves without Protozoa ( $n=260$ ) is of type:  $P_{ls}=A_{ls}M^{1.0089\pm 0.042}$  with  $R^2=0.897$ ,  $A_{ls}=14.16\times 10^5$  kJ/kg,  $SE=\pm 0.042$ , and 95% confidence interval of exponent (0.967-1.051). In all combinations between Ectotherms, Mammals and Aves the exponent is near to 1.0. The linear coefficient  $A_{ls}$  is the total metabolic energy, exhausted during the lifespan per 1kg body mass of given organism and appears to be relatively constant parameter, because of rising 10 times only from Ectotherms to Mammals and Aves, despite of 21 orders of magnitude difference between body mass of organisms.

**Key words:** scaling, metabolic energy, lifespan, ectotherms, mammals, aves

**INTRODUCTION**

The patterns existing between the fundamental characters of living organisms and their body mass are generally described as a power function. The bioenergetic studies of Kleiber [1], Brody et al. [2], Zeuthen [3], Hemmingsen [4], Kleiber [5], Schmidt-Nielsen [6], McNab [7], Heusner [8], Niklas [9], Nagy [10] and da Silva and Barbosa [11] on Ectotherms, Mammals and Aves have shown that the basal metabolic rate ( $P$ , kJ/d) in animals is related to the body mass ( $M$ , kg) by the equation:

$$P=aM^k \quad (1)$$

where  $a$  is the normalization constant, and  $k$  is the allometric scaling exponent. One of the most important points of controversy in the scientific discussion about the power function is focused on the value of the scaling exponent.

Some researchers consider the power function (1) with exponent  $k=0.75$  as a universal scaling law, generalized to all living organisms and forms of life (Hemmingsen [4], Kleiber [5], Feldman and McMahon [12], West et al. [13-14], Banavar et al. [15], Savage et al. [16]). On the other hand, several recent studies provided evidences, supporting certain variability in the exponent of the allometric scaling law (Riisgård [17], Dodds et al. [18], Bokma [19], Agutter and Wheatley [20], Glazier [21], Reich et al. [22], White and Seymour [23], White *et al.* [24]).

The values of the scaling exponent  $k$  have been studied in other experimental conditions for all animal groups.

Zeuthen[3] and Hemmingsen [4] show that the exponent  $k$  is equal to 0.75 in unicellular Eukaryotes. As a hole, unicellular organisms (Eukaryotes and Prokaryotes) showed isometric scaling with exponent  $k=1.0$  [25].

Accordingly to Galvão [26], Ultsch [27], Prosser [28], Schmidt-Nielsen [6], Tudge [29]

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and Makarieva *et al.* [30] the exponent  $k$  varied in the interval 0.6-1.0 in Ectotherms.

The data of Kleiber [1, 5], McNab [7], Heusner [8], Agutter and Wheatley [20], White and Seymour [23], White *et al.* [24] shown that in Mammals the exponent  $k$  varied in the interval 0.602-0.87.

The data of Lasiewski and Dawson [31-32], Aschoff and Pohl [33], Bennet and Harvey [34], Nagy *et al.* [35], Rezende [36], Nagy [10] and Rottenberg [37] shown that in Aves the exponent  $k$  varied in the interval 0.67-0.734.

Thus, the scaling exponent in Ectotherms, Mammals and Aves varied in the interval 0.6-1.0.

The allometric relationship between the lifespan of living organisms ( $T_{ls}$ , years) and the body mass ( $M$ , kg) in other evolutionary groups have been expressed also as a power relationship:

$$T_{ls} = bM^n \quad (2)$$

where  $b$  is the normalization constant, and  $n$  is the allometric scaling exponent. Some researchers, including Fenchel [38], Ernest [39], Brown *et al.* [40], Damuth [41], Ginsburg and Damuth [42] consider the power law (2) with scaling exponent  $n=0.25$ , as a universal scaling law for all living organisms and forms of life. The values of the exponent  $n$  have been studied for all animals groups. For Ectotherms the exponent  $n$  falls in the interval 0.16-0.30, according to Bonner [43], Günther [44], Prosser [28], Schmidt-Nielsen [6] and Smith-Sonneborn [45]. For Mammals, the exponent  $n$  falls in the interval 0.15-0.3, according to Sacher [46], Mallouk [47], Cutler [498] and Speakman *et al.* [49]. For Aves the exponent  $n$  falls in the interval 0.19-0.216, according to Lindstedt and Calder [50-51], Nagy [10], Rottenberg [37], Møller [52] and Bonduriansky [53]. Thus, the scaling exponent  $n$  in Ectotherms, Mammals and Aves varied in the interval 0.15-0.3.

Different approaches are available to study the relationship between the total metabolic energy per lifespan and the body mass of animals. The first approach is based on the hypothesis of Rübner [54], that the mass-specific expenditure of the energy per lifespan is relatively constant ( $C$ ) in different animals, i. e.:

$$(P/M)T_{ls} = C \quad (3)$$

The hypothesis of Rübner continues being studied for about 100 years, since it was formulated in 1908, because of its fundamentality. Many researchers like Boddington [55] and Speakman [56] discussed this idea theoretically or presented data supporting it or against it. The invariability of the ratio:

$$(P/M)T_{ls} = CM^\alpha \quad (4)$$

where  $C$  is the normalization constant and  $\alpha$  is the allometric scaling exponent, has been studied from Speakman [56-57] and Nagy [58]. From mathematical point of view, the exponent  $\alpha = 0$  results in independence from the mass  $M$ , because  $M^\alpha = 1$  and the equation (4) would still result in a constant value. A tentative evaluation of Speakman [56] for Mammals and Aves showed that  $\alpha$  varied in interval from -0.08 to 0.08. Regarding the combination between the basal metabolic rate and the maximum lifespan, Speakman calculated for Mammals  $\alpha = -0.0734$  ( $R^2 = 0.07$ ) and for Aves  $\alpha = -0.109$  ( $R^2 = 0.126$ ).

The 'rate of living' theory of Pearl [59] postulated also that the mass-specific expenditure of energy per lifespan is relatively constant ( $C$ ) between animals i.e. the product  $(P/M)T_{ls} = C$ . Because the quotient for invariability in the lifetime expenditure of energy per unit body mass of tissue is not based on statistics, Speakman [56] combined the data about daily energy expenditure in free-living animals, measured by doubly-labelled water method of Nagy [58] and Speakman [57], with the data for maximum lifespan of Carey and Judge [60]. This combination allowed test statistically the 'rate of living' theory. In this case Speakman [56] calculated for Mammals  $\alpha = -0.208$  ( $R^2 = 0.377$ ), for Aves  $\alpha = -0.0696$  ( $R^2 = 0.056$ ) and received a significant negative association between residual lifespan and residual daily energy expenditure. Namely, the Mammals that had high rates of expenditure for their body mass died sooner. The results of other authors for birds, like Rottenberg [37], revealed some evidences in support of 'rate of living' theory for Mammals and Aves.

A recent approach to study the relationship between the total metabolic energy per lifespan and the body mass of animals [61-65] concerned the study of the direct statistical

relationship between the total metabolic energy per lifespan ( $P_{ls} = PT_{ls}$ ) and the body mass ( $M$ ) of animals i.e. the calculation of the function:

$$PT_{ls} = A_{ls} M^r \quad (5)$$

where  $A_{ls}$  is a coefficient and  $r$  is a exponent.

In recent publications Atanasov [61-62] showed that for Ectotherms the coefficient  $A_{ls}$  varied in interval of  $(2.34-3.7) \times 10^5$  kJ/kg, the exponent  $r$  varied in interval of 0.97-1.084 and  $R^2$  falls in interval of 0.97-0.98. For Mammals [63] the coefficient  $A_{ls}$  varied in interval of  $(7.15-11.4) \times 10^5$  kJ/kg, the exponent  $r$  varied in interval of 0.97-1.05 and  $R^2$  varied in interval of 0.98-0.983. For Aves [64-65] the coefficient  $A_{ls}$  varied in interval of  $(26.8-37.2) \times 10^5$  kJ/kg, the exponent  $r$  varied in interval of 0.88-0.939 and  $R^2$  varied in interval of 0.97-0.98. In all cases the exponent  $r$  varied around 1.0 in the interval of 0.88-1.084.

The aim of this study is to establish and calculate the coefficient  $A_{ls}$  and exponent  $r$  in relationship (5) between the total metabolic energy per lifespan and the body mass in a wide range of animals - 278 Ectotherms, Mammals and Aves (all together) with about a 21 order of magnitude variation between the body mass.

## DATA AND METHODS

All data for the 278 studied individuals are shown in **Table 1**.

The data for the Ectothermic individuals – the body mass ( $M$ , kg), the basal metabolic rate ( $P$ , kJ/day), the temperature ( $t^\circ\text{C}$ ), the lifespan ( $T_{ls}$  in years and day) and the total metabolic energy per lifespan ( $P_{ls}$ , kJ) were taken by paper of Atanasov [61-62] and Fujiwara [66]. Included are the data for 18 unicellular and 38 multicellular ectotherms from the orders of Protozoa, Nematoda, Mollusca, Asteroidae, Arthropoda (Arachnoidae, Insecta), Isopoda (Crustacea), Osteichthytes, Amphibia and Reptilia.

The data for the Mammals were taken by Atanasov [63] and Carey and Judge [60] and involves 95 species, including 3 monotremes (Subclass Prototheria), 16 marsupialis (Subclass Theria, Infraclass Metatheria) and 76 “placentals” (Subclass Theria, Infraclass Eutheria) from orders: Monotremata, Didelphoidea, Dasyurida, Syndactyla, Xenarthra, Pholidota Soricomorpha, Rodentia,

Lagomorpha, Artiodactyla, Carnivora, Pinnipedia, Chiroptera and Primates.

The data for Nonpasseriformes Aves were taken by Atanasov [64] and Gregory [67], involving 95 Nonpasseriformes species from the orders of Struthioniformes, Rheiformes, Casuariiformes, Apterygiformes, Sphenisciformes, Procellariiformes, Pelecaniformes, Ciconiiformes, Anseriformes, Charadriiformes, Columbiformes, Falconiformes, Galliformes, Gruiformes, Psittaciformes, Cuculiformes, Strigiformes, Caprimulgiformes, Apodiformes, Coliiformes, Trogoniformes, Coraciiformes, Piciformes.

The data for the 32 Passeriformes were taken by Atanasov [65].

For each organism or animal the total metabolic energy per lifespan  $P_{ls}$  is calculated as a product between the basal metabolic rate  $P$  (kJ/day) and the lifespan  $T_{ls}$  (day):

$$P_{ls}(\text{kJ}) = PT_{ls} \quad (6)$$

For each organism the total metabolic energy per lifespan, per 1kg body mass is calculated as a ratio between  $P_{ls}$  (kJ) and the body mass  $M$  (kg):

$$A_{ls}(\text{kJ/kg}) = P_{ls}/M \quad (7)$$

Least-square regression analyses were performed using STATISTICA ([www.statsoft.com](http://www.statsoft.com)). Logarithm of total metabolic energy per lifespan  $P_{ls}$  were regressed against logarithm of body mass  $M$ , after that the results were presented in  $P_{ls} - M$  functional relationship. The linear coefficient  $A_{ls}$ , the correlation coefficient  $R$ , the exponent  $r$ , the standard error of the exponent  $SE$  and the 95% confidence interval  $CI$  were calculated for Ectotherms, Mammals and Aves (in common and separately).

Analyses of covariance ANCOVA ([www.statsoft.com](http://www.statsoft.com)) were used for estimation of P-level of the correlation between the total metabolic energy per lifespan and the body mass for Ectotherms, Mammals and Aves (in common and separately) by Student's t-test for  $p=0.00001$ .

## RESULTS

In data set for Ectotherms (from Bacteria to Alligator) the body mass  $M$ , the basal metabolic rate  $P$ , the lifespan  $T_{ls}$  and the total

metabolic energy per lifespan  $P_{ls}$  in **Table 1** varied in the intervals of ( $6 \times 10^{-17}$  - 49)kg, ( $1.58 \times 10^{-10}$  - 1830)kJ/day, 20min - 40years and ( $2.22 \times 10^{-12}$  -  $267 \times 10^5$ )kJ.

In the data set for Mammals (from *Antechinomus laniger* to *Elephas maximum*)  $M$ ,  $P$ ,  $T_{ls}$  and  $P_{ls}$  varied in the intervals of (0.0085-3000)kg, ( $5.166-165 \times 10^3$ )kJ/day, (2-54)years and ( $3.77 \times 10^3-32.52 \times 10^8$ )kJ.

In data set for Aves (from *Calypte costae* to *Struthio camelus*)  $M$ ,  $P$ ,  $T_{ls}$  and  $P_{ls}$  varied in the intervals of (0.0032-100)kg, (4.476-9823)kJ/day, (4-45)years and ( $14.45 \times 10^3-161 \times 10^6$ ) kJ. Thus, the range of variation of the body mass between all 278 individuals was  $3 \times 10^{21}$  times, the variation of the basal metabolic rate is  $1 \times 10^{16}$  times, the variation of the lifespan is  $1 \times 10^6$  times and the variation of the total metabolic energy per lifespan was  $6 \times 10^{18}$  times.

**Table 1.** Data for body mass ( $M$ ), basal metabolic rate ( $P$ ), lifespan ( $T_{ls}$ ), total metabolic energy per lifespan ( $PT_{ls}$ ) and temperature ( $t$ )° for Ectotherms, Mammals and Aves.

N	CLASS, ORDER, SPECIES	M(kg)	P(kJ/day)	T(d, y)	PT <sub>ls</sub> (kJ)	t(°C)
	<b>ECTOTHERMS</b>					
	<i>Unicellular organisms</i>					
1.	<i>Hemophilus</i>	$6.1 \times 10^{-17}$	$1.068 \times 10^{-9}$	0.0207d	$2.223 \times 10^{-11}$	30°
2.	<i>Diplococcus</i>	$3.8 \times 10^{-16}$	$4.383 \times 10^{-9}$	0.0175d	$7.68 \times 10^{-11}$	30°
3.	<i>Escherichia</i>	$3.9 \times 10^{-16}$	$4.384 \times 10^{-9}$	0.0138d	$6.08 \times 10^{-11}$	25°
4.	<i>Shigella</i>	$7.1 \times 10^{-16}$	$6.85 \times 10^{-9}$	0.016d	$1.1 \times 10^{-10}$	25°
5.	<i>Staphylococcus</i>	$7.8 \times 10^{-16}$	$7.41 \times 10^{-9}$	0.0186d	$1.377 \times 10^{-10}$	30°
6.	Bacteria	$1 \times 10^{-15}$	$48 \times 10^{-11}$ (max)	1/48d	$1 \times 10^{-11}$	25°
7.	Bacteria	$1 \times 10^{-15}$	$24 \times 10^{-11}$ (min)	1d	$24 \times 10^{-12}$	25°
8.	<i>Azotobacter chroococcum</i>	$1 \times 10^{-15}$	$4.8 \times 10^{-10}$	1/24d	$2 \times 10^{-11}$	30°
9.	<i>Bacillus</i>	$4.3 \times 10^{-15}$	$2.635 \times 10^{-8}$	0.0244d	$6.432 \times 10^{-10}$	30°
10.	<i>Saccharomyces cerevisiae</i>	$2 \times 10^{-14}$	$36.2 \times 10^{-11}$	1/24d	$1.5 \times 10^{-11}$	20°
11.	Flagellata and Mastogophora	$1 \times 10^{-13}$	$30 \times 10^{-10}$ (max)	1d	$3.0 \times 10^{-9}$	20°
12.	Flagellata and Mastogophora	$1 \times 10^{-13}$	$3 \times 10^{-10}$ (min)	7d	$2.1 \times 10^{-9}$	20°
13.	Euglena	$8 \times 10^{-12}$	$7.4 \times 10^{-6}$	0.438d	$3.24 \times 10^{-6}$	25°
14.	Chlamydomonas	$4 \times 10^{-12}$	$4.4 \times 10^{-6}$	0.4d	$1.76 \times 10^{-6}$	25°
15.	Tetrahymena	$2 \times 10^{-11}$	$2.55 \times 10^{-5}$	0.124d	$3.162 \times 10^{-6}$	25°
16.	Paramecium	$4 \times 10^{-10}$	$2.33 \times 10^{-4}$	0.33d	$7.7 \times 10^{-5}$	25°
17.	Amoeba	$2 \times 10^{-8}$	$5 \times 10^{-2}$	2d	$1.0 \times 10^{-1}$	25°
18.	Stentor	$8 \times 10^{-8}$	$7.4 \times 10^{-2}$	2d	$1.48 \times 10^{-1}$	25°
	<b>Nematoda</b>					
19	<i>Clymenella torquata</i>	$50 \times 10^{-6}$	$7.1 \times 10^{-3}$	6y	15.5	20°
20	<i>Clymenella mucoza</i>	$109 \times 10^{-6}$	$13.9 \times 10^{-3}$	6y	30.5	20°
21	<i>Clymenella zonalis</i>	$23 \times 10^{-6}$	$3.6 \times 10^{-3}$	6y	7.8	20°
22	<i>Ascaris suum</i>	$1 \times 10^{-5}$	$2.412 \times 10^{-3}$	4y	3.524	20°
	<b>Mollusca</b>					
23	<i>Ancylus fluviatilis</i>	$2 \times 10^{-5}$	$1.707 \times 10^{-3}$	8y	4.984	16°
24	<i>Haliotis rufescens</i>	$3 \times 10^{-3}$	0.1733	10y	630	16°
	<b>Asteroidae</b>					
25	<i>Asterias rubens</i> (sea star)	$10 \times 10^{-3}$	1.93	7y	$4.93 \times 10^3$	11°
	<b>Arthropoda (Arachnoidae)</b>					
26	Spider ( <i>Phidiphor</i> )	$3.37 \times 10^{-4}$	$24.12 \times 10^{-3}$	6y	52.5	17°
27	Spider ( <i>Achaeranea</i> )	$0.73 \times 10^{-4}$	$12.54 \times 10^{-3}$	5y	22.85	17°
28	Aranei spider ( <i>Phidippus audax</i> )	$5.68 \times 10^{-4}$	$25.48 \times 10^{-3}$	10y	93	17°
	<b>Arthropoda (Insecta)</b>					
29	<i>Lepisma saccharina</i>	$1.25 \times 10^{-6}$	$8.5 \times 10^{-3}$	24d	0.204	17°
30	<i>Drozofila melanogaster</i>	$1.2 \times 10^{-6}$	$8.4 \times 10^{-3}$	24d	0.202	20°
	<b>Arthropoda, Isopoda (Crustacea)</b>					
31	<i>Emerita portoricensis</i>	$15 \times 10^{-3}$	$796 \times 10^{-3}$	10y	$2.9 \times 10^3$	20°
32	<i>Orcomella</i>	$2.4 \times 10^{-3}$	$203 \times 10^{-3}$	10y	740.65	17°
33	<i>Laborchestia</i>	$2.7 \times 10^{-4}$	$22.92 \times 10^{-3}$	10y	83.671	20°
	<b>Osteichthytes (Pisces)</b>					
34	<i>Notothenia coriiceps</i>	0.2	5.4	24y	$47.3 \times 10^3$	0°

35	<i>Chaenocephalus aceratus</i>	0.2	6.07	24y	$53.2 \times 10^3$	$0^0$
36	<i>Mugil cephalus</i>	0.149	7.19	18y	$47.2 \times 10^3$	$14^0$
37	<i>Girella nigricans</i>	0.070	4.42	12y	$19.7 \times 10^3$	$20^0$
38	<i>Anguilla anguilla</i>	0.040	1.698	12y	$7.4 \times 10^3$	$17^0$
39	<i>Bagarius bagarius</i>	0.147	6.52	25y	$59.5 \times 10^3$	$17^0$
40	<i>Salvelinus alpinus</i>	0.112	11.075	12y	$48.5 \times 10^3$	$18^0$
	<b>Amphibia</b>					
41	Frog ( <i>Rana</i> )	$32 \times 10^{-3}$	0.852	36y	$11.2 \times 10^3$	$15^0$
42	Frog ( <i>Acris</i> )	$30 \times 10^{-3}$	1.447	25y	$13.2 \times 10^3$	$15^0$
43	Salamandra ( <i>Salamandra atra</i> )	$13.4 \times 10^{-3}$	0.482	20y	$3.5 \times 10^3$	$14^0$
	<b>Reptilia</b>					
44	Reptilia ( <i>Amphibolurus</i> )	$373 \times 10^{-3}$	25.18	10y	$9.2 \times 10^4$	$28^0$
45	Reptilia ( <i>Dipsosaurus</i> )	$64 \times 10^{-3}$	0.965	10y	$3.5 \times 10^3$	$20^0$
46	Reptilia ( <i>Lasepta</i> )	$6.3 \times 10^{-3}$	0.744	10y	$2.72 \times 10^3$	$19^0$
47	Tortoise ( <i>Chrysemys</i> )	0.25	4.48	30y	$4.9 \times 10^4$	$18^0$
48	Sauria ( <i>Iguana</i> )	0.785	58.7	20y	$4.3 \times 10^5$	$20^0$
49	Crocodile ( <i>Alligator</i> )	49	$1.83 \times 10^3$	40y	$267 \times 10^5$	$28^0$
	<b>Reptilia (Snakes)</b>					
50	Boidae	1.0	10	30y	$109.5 \times 10^3$	$18^0$
51	Boa	10	100	30y	$109.5 \times 10^4$	$18^0$
52	Colubridae	0.080	1	14y	$5 \times 10^3$	$18^0$
53	Piton	5	17	30y	$1.86 \times 10^5$	$18^0$
54	Eunectes	11.3	114.5	30y	$12.53 \times 10^5$	$20^0$
55	Natrix	0.084	2.834	14y	$14.5 \times 10^3$	$16^0$
56	Grass-snake	3.27	28.4	30y	$3.11 \times 10^5$	$17^0$
	<b>MAMMALS</b>					
	<b>Monotremata</b>					
57	<i>Tachiglossus aculeatus</i>	2.5	301.5	14y	$15.4 \times 10^5$	$30-31^0$
58	<i>Zaglossus bruijni</i>	10.3	593.78	20y	$43.34 \times 10^5$	$30-31^0$
59	<i>Ornithorhynchus anatinus</i>	1.3	228.6	9y	$7.51 \times 10^5$	$30-31^0$
	<b>Didelphoidea</b>					
60	<i>Lutreolina crassicaudata</i>	0.812	195.85	5y	$3.57 \times 10^5$	$36^0$
61	<i>Didelphis marsupialis</i>	1.329	298.66	6y	$6.54 \times 10^5$	$36^0$
62	<i>Didelphis virginiana</i>	3.257	518.5	8y	$15.14 \times 10^5$	$36^0$
	<b>Dasyurida</b>					
63	<i>Antechinus macdonnellensis</i>	$14.1 \times 10^{-3}$	9	2y	$6.57 \times 10^3$	$36^0$
64	<i>Antechinus stuartii</i>	$36.5 \times 10^{-3}$	17.6	2.5y	$16.06 \times 10^3$	$36^0$
65	<i>Antechinomus laniger</i>	$8.5 \times 10^{-3}$	5.166	2y	$3.77 \times 10^3$	$36^0$
66	<i>Dasyuroides byrnei</i>	$89 \times 10^{-3}$	37.35	3y	$40.89 \times 10^3$	$36^0$
67	<i>Isodon macroourus</i>	1	200.9	8y	$5.87 \times 10^5$	$36^0$
68	<i>Perameles nasuta</i>	0.645	152.46	7y	$3.9 \times 10^5$	$36^0$
69	<i>Sminthopsis crassicaudata</i>	$15 \times 10^{-3}$	9.64	2y	$7 \times 10^3$	$36^0$
70	<i>Planigale maculata</i>	$13 \times 10^{-3}$	13.65	1.5y	$7.47 \times 10^3$	$36^0$
71	<i>Sacrophilus harrisii</i>	5.05	628.11	10y	$22.926 \times 10^5$	$36^0$
	<b>Syndactyla</b>					
72	<i>Trichosurus vulpecula</i>	1.982	305.5	8y	$8.9 \times 10^5$	$37^0$
73	<i>Macropus robustus</i>	4.69	693.9	11y	$25.7 \times 10^5$	$37^0$
74	<i>Macropus rufus</i>	40	$4 \times 10^3$	15y	$21.9 \times 10^6$	$37^0$
75	<i>Macropus eugenii</i>	4.796	671	11y	$26.94 \times 10^5$	$37^0$
	<b>Xenarthra</b>					
76	<i>Bradypus variegatus</i>	3.79	331	19y	$22.95 \times 10^5$	$37^0$
77	<i>Dasybus novemcinctus</i>	3.32	384.4	10y	$14 \times 10^5$	$37^0$
	<b>Pholidota</b>					
78	<i>Manis tricuspis</i>	2.73	439.7	8y	$12.8 \times 10^5$	$37^0$
79	<i>Manis javanica</i>	4.22	529.3	11y	$21.25 \times 10^5$	$37^0$
	<b>Soricomorpha</b>					
80	<i>Blarina brevicauda</i>	$21 \times 10^{-3}$	25.326	1.2y	$11.09 \times 10^3$	$37^0$
	<b>Insectivora</b>					
81	<i>Sorex caecutiens</i>	$3.6 \times 10^{-3}$	15	0.8y	$4.32 \times 10^3$	$37.9^0$
82	<i>Sorex araneus</i>	$5.0 \times 10^{-3}$	17.64	0.8y	$5.08 \times 10^3$	$37.9^0$

	<b>Rodentia</b>					
83	<i>Cricetus cricetus</i>	0.362	111.75	4y	$16.3 \times 10^4$	37.8°
84	<i>Liomys salvini</i>	$43.8 \times 10^{-3}$	22.51	2.5y	$20.63 \times 10^3$	37.8°
85	<i>Liomys irroratus</i>	$48.1 \times 10^{-3}$	25.99	2.5y	$23.72 \times 10^3$	37.8°
86	<i>Microtus minutus</i>	$9.8 \times 10^{-3}$	17.97	0.8y	$5.175 \times 10^3$	37.9°
87	<i>Microtus mexicanus</i>	$28 \times 10^{-3}$	22	1.5y	$12 \times 10^3$	37.8°
88	<i>Ochrotomys nuttalli</i>	$19.5 \times 10^{-3}$	23.78	1.5y	$12.84 \times 10^3$	37.8°
89	<i>Mus musculus</i>	0.021	20.9	1.5y	$1.14 \times 10^4$	37.8°
90	<i>Neotoma cirenea</i>	0.321	120.78	3.5y	$15.43 \times 10^4$	37.8°
91	<i>Neotoma lepida</i>	0.139	48.24	3.5y	$6.16 \times 10^5$	37.8°
92	<i>Neotoma fuscipes</i>	0.187	71.27	3.5y	$9.1 \times 10^4$	37.8°
93	<i>Neotoma albigula</i>	0.172	61.4	3.5y	$7.84 \times 10^4$	37.8°
94	<i>Ondatra zibethicus</i>	0.842	333	3.5y	$42.54 \times 10^4$	37.8°
95	<i>Perognathus longimembris</i>	$11.5 \times 10^{-3}$	11.428	1.5y	$6.25 \times 10^3$	37.8°
96	<i>Perognathus hispidus</i>	$39.5 \times 10^{-3}$	23.82	2y	$17.387 \times 10^3$	37.8°
97	<i>Peromyscus eremicus</i>	$21.5 \times 10^{-3}$	15.35	1.5y	$8.4 \times 10^3$	37.8°
98	<i>Peromyscus californicus</i>	$45.5 \times 10^{-3}$	22.61	2.5y	$20.63 \times 10^3$	37.8°
99	<i>Peromyscus leucopus</i>	$22.2 \times 10^{-3}$	26.77	1.5y	$12.15 \times 10^3$	37.8°
100	<i>Chinchilla laniger</i>	0.494	111.99	8y	$3.27 \times 10^5$	37.8°
101	<i>Lagostomus maximus</i>	6.784	916.36	13y	$43.48 \times 10^5$	38°
102	<i>Kerodon rupestris</i>	0.750	193	6y	$422.97 \times 10^3$	37.8°
103	<i>Cavia porcellus</i>	0.5	192	6y	$4.2 \times 10^5$	37.8°
104	<i>Marmota monax</i>	2.65	319.6	10y	$11.665 \times 10^5$	38°
105	<i>Rattus fuscipes</i>	0.076	40.68	3y	$445.5 \times 10^2$	37.8°
106	<i>Rattus lutreolus</i>	0.109	30.49	3.5y	$3.9 \times 10^4$	37.8°
107	<i>Rattus rattus</i>	0.132	80.86	3.5y	$10.33 \times 10^4$	37.8°
108	<i>Rattus sordidus</i>	0.187	51.4	4y	$75.04 \times 10^3$	37.8°
109	<i>Sigmodon hispidus</i>	0.161	168.4	3y	$1.6 \times 10^5$	37.8°
	<b>Lagomorpha</b>					
110	<i>Lepus europaeus</i>	2.5	528	8y	$15.4 \times 10^5$	38°
111	<i>Lepus americanus</i>	1.528	686.4	7y	$17.54 \times 10^5$	38°
112	<i>Lepus californicus</i>	2.3	632.3	8y	$18.4 \times 10^5$	38°
113	<i>Lepus timidus</i>	3.004	521.6	9y	$17.1 \times 10^5$	38°
114	<i>Lepus alleni</i>	3.362	729.8	9y	$23.97 \times 10^5$	38°
115	<i>Sulvilagus audubonii</i>	0.702	220.12	7y	$5.62 \times 10^5$	37.8°
	<b>Artiodactyla</b>					
116	<i>Antilopa americana</i>	32	4 322	18y	$28.4 \times 10^6$	37.9°
117	<i>Camelus dromedarius</i>	407	23 630	26y	$224.25 \times 10^6$	37.8°
118	<i>Elephas maximum</i>	$3 \times 10^3$	$165 \times 10^3$	54y	$32.52 \times 10^8$	36°
119	<i>Capreolus capreolus</i>	19	3 666	13y	$17.4 \times 10^6$	37.9°
120	<i>Cervus elaphus</i>	58	$7.8 \times 10^3$	18y	$51.2 \times 10^6$	37.9°
121	<i>Equus caballus</i>	400	32 000	40y	$4.67 \times 10^8$	37.8°
122	<i>Ovis aries</i>	49	4 200	20y	$30.7 \times 10^6$	37.9°
123	<i>Ovis canadensis</i>	65	10 660	20y	$77.8 \times 10^6$	37.9°
124	<i>Bubalus caffer</i>	420	29 400	35y	$37.5 \times 10^7$	37.8°
125	<i>Rupicapra rupicapra</i>	40	3 140	21y	$24.07 \times 10^6$	37.9°
126	<i>Sus scrofa</i>	140	$12 \times 10^3$	15y	$65.7 \times 10^6$	37.8°
127	<i>Tayassu tajacu</i>	20.2	2 826	15y	$15.47 \times 10^6$	37.9°
	<b>Carnivora</b>					
128	<i>Lutra lutra</i>	10	2 200	15y	$120.4 \times 10^5$	37.9°
129	<i>Gulo gulo</i>	12.7	2 818	15y	$154.29 \times 10^5$	37.9°
130	<i>Meles meles</i>	11.05	1 439.2	16y	$84.05 \times 10^5$	37.9°
131	<i>Enhydra lutris</i>	40	$12.35 \times 10^3$	16y	$721.2 \times 10^5$	37.9°
132	<i>Vulpes vulpes</i>	5.01	1 208.4	12y	$5.29 \times 10^6$	38°
133	<i>Canis latrans</i>	10	1 320.5	18y	$86.76 \times 10^5$	38°
134	<i>Canis familiaris</i>	14	1 881	18y	$123.6 \times 10^5$	37.9°
135	<i>Panthera onca</i>	18	2 436	20y	$177.8 \times 10^5$	37.9°
136	<i>Felis silvestris</i>	3	546	11y	$21.9 \times 10^5$	38°
137	<i>Mustela vison</i>	0.66	238.6	8y	$6.97 \times 10^5$	37.8°
	<b>Pinnipedia</b>					

138	<i>Phoca vitulina</i>	26	7 400	13y	35.1×10 <sup>6</sup>	37.9°
139	<i>Delphinapterus leucas</i>	170	22 962	25y	209.5×10 <sup>6</sup>	37.8°
140	<i>Hyperoodon ampullatus</i>	1 000	69.46 ×10 <sup>3</sup>	40y	1014 ×10 <sup>6</sup>	37.8°
	<b>Chiroptera</b>					
141	<i>Desmodus rotundus</i>	0.029	9.65	8y	28.18×10 <sup>3</sup>	37.8°
142	<i>Vampyrops lineatus</i>	0.022	15.6	6y	34.16×10 <sup>3</sup>	37.8°
143	<i>Macroderma gigas</i>	0.148	67.97	19y	2.48×10 <sup>5</sup>	37.8°
144	<i>Eumops perotis</i>	0.057	14.2	10y	51.83×10 <sup>3</sup>	37.8°
145	<i>Pteropus policephalus</i>	0.598	153	13y	7.26×10 <sup>5</sup>	37.8°
	<b>Primates</b>					
146	<i>Pan troglodytes</i>	45	4.62×10 <sup>3</sup>	40y	67.45×10 <sup>6</sup>	37.9°
147	<i>Macaca mulatta</i>	5	960	25y	86.4×10 <sup>5</sup>	38°
148	<i>Pongo pygmaeus</i>	150	15.54×10 <sup>3</sup>	45y	251.75×10 <sup>6</sup>	37.8°
149	<i>Gorilla gorilla</i>	250	21×10 <sup>3</sup>	45y	340×10 <sup>6</sup>	37.8°
150	<i>Hylobater lar</i>	8	1 512	25y	136×10 <sup>5</sup>	38°
151	<i>Homo sapiens</i>	65	7.56×10 <sup>3</sup>	75y	204×10 <sup>6</sup>	37.9°
	<b>AVES</b>					
	<b>Struthioniformes</b>					
152	<i>Struthio camelus</i>	100	9 823	45y	161.3×10 <sup>6</sup>	40°
153	<i>Struthio camelus</i>	100	5 442.36	45y	89.4×10 <sup>6</sup>	40°
	<b>Rheiformes</b>					
154	<i>Rhea americana</i>	21.7	3 344	50y	61×10 <sup>6</sup>	40°
	<b>Casuariiformes</b>					
155	<i>Casuarus bennetti</i>	17.6	2 156.9	50y	39.36×10 <sup>6</sup>	40°
156	<i>Dromiceus novaehollandiae</i>	38.925	3 746.1	45y	61.5×10 <sup>6</sup>	40°
	<b>Apterygiformes</b>					
157	<i>Apteryx australis</i>	2.38	347.77	28y	35.5×10 <sup>5</sup>	40°
158	<i>Apteryx owenii</i>	1.095	178.486	24y	15.65×10 <sup>5</sup>	40°
159	<i>Apteryx haasti</i>	2.54	360.734	28y	36.86×10 <sup>5</sup>	40°
	<b>Sphenisciformes</b>					
160	<i>Pygoscelis papua</i>	6.29	1 603.45	35y	20.48×10 <sup>6</sup>	40°
161	<i>Pygoscelis adeliae</i>	3.97	1 055.87	32y	12.3×10 <sup>6</sup>	40°
162	<i>Eudyptes pachyrhynchus</i>	2.6	597.32	28y	61×10 <sup>5</sup>	40°
163	<i>Eudyptes chrysocome</i>	2.506	862	28y	88×10 <sup>5</sup>	40°
164	<i>Eudyptes crestatus</i>	2.33	503.7	28y	51.5×10 <sup>5</sup>	40°
165	<i>Eudyptula albosignata</i>	1.15	570.57	24y	50×10 <sup>5</sup>	40°
	<b>Procellariiformes</b>					
166	<i>Macronectus giganteus</i>	3.63	1 492.68	30y	16.3×10 <sup>6</sup>	40°
167	<i>Pterodroma hypoleuca</i>	0.18	89.87	15y	4.92×10 <sup>5</sup>	40°
168	<i>Pterodroma mollis</i>	0.274	150.9	18y	9.9×10 <sup>5</sup>	40°
169	<i>Pachyptila salvini</i>	0.165	133.76	15y	7.32×10 <sup>5</sup>	40°
170	<i>Puffinus griseus</i>	0.740	249.13	18y	16.36×10 <sup>5</sup>	40°
	<b>Pelecaniformes</b>					
171	<i>Pelecanus occidentalis</i>	3.038	894.5	35y	11.4×10 <sup>6</sup>	40°
172	<i>Sula dactylatra</i>	1.289	475.26	29y	50.3×10 <sup>5</sup>	40°
173	<i>Sula sula</i>	1.017	375.78	28y	38.4×10 <sup>5</sup>	40°
174	<i>Phalacrocorax auritus</i>	1.33	474	29y	50.2×10 <sup>5</sup>	40°
	<b>Ciconiiformes</b>					
175	<i>Ardea herodias</i>	1.87	535	31y	60.54×10 <sup>5</sup>	40°
176	<i>Hydranassa tricolor</i>	0.31	147.55	18y	9.5×10 <sup>5</sup>	40°
177	<i>Mysteria americana</i>	2.5	840.18	33y	101.2×10 <sup>5</sup>	40°
178	<i>Leptoptilos javanicus</i>	5.71	1 283.2	39y	182.66×10 <sup>5</sup>	40°
	<b>Anseriformes</b>					
179	<i>Cygnus buccinator</i>	8.88	1 747.24	40y	255×10 <sup>5</sup>	40°
180	<i>Branta bernicla</i>	1.168	390.4	29y	41.3×10 <sup>5</sup>	40°
181	<i>Aix sponsa</i>	0.485	271.7	24y	23.8×10 <sup>5</sup>	40°
182	<i>Anas platyrhynchos</i>	1.1323	434.7	25y	39.6×10 <sup>5</sup>	40°
183	<i>Anas crecca</i>	0.25	143.8	20y	10.5×10 <sup>5</sup>	40°
184	<i>Anas querquedula</i>	0.289	192.7	20y	14×10 <sup>5</sup>	40°
185	<i>Aythya fuligula</i>	0.574	233.2	20y	17×10 <sup>5</sup>	40°

	<b>Charadriiformes</b>					
186	<i>Tringa ochropus</i>	0.09	79.4	10y	$2.9 \times 10^5$	40°
187	<i>Stercorarius skua</i>	0.97	409.6	25y	$37.4 \times 10^5$	40°
188	<i>Larus delawarensis</i>	0.439	249.13	20y	$18.2 \times 10^5$	40°
189	<i>Larus occidentalis</i>	0.761	293	20y	$21.3 \times 10^5$	40°
190	<i>Gygis alba</i>	0.0981	70.22	15y	$3.84 \times 10^5$	40°
	<b>Columbiformes</b>					
191	<i>Columba unicincta</i>	0.318	148	20y	$10.8 \times 10^5$	40°
192	<i>Columba livia</i>	0.315	150	20y	$10.95 \times 10^5$	40°
193	<i>Columba livia</i>	0.266	140.87	20y	$10.3 \times 10^5$	40°
194	<i>Streptopelia decaocto</i>	0.187	110	20y	$8.03 \times 10^5$	40°
	<b>Falconiformes</b>					
195	<i>Vultur gryphus</i>	10.32	1 467.18	40y	$21.4 \times 10^6$	40°
196	<i>Falco sparverius</i>	0.117	72.73	15y	$4 \times 10^5$	40°
197	<i>Accipiter nisus</i>	0.135	81.93	19y	$5.68 \times 10^5$	40°
198	<i>Buteo buteo</i>	1.012	324.37	28y	$33.15 \times 10^5$	40°
199	<i>Gypaetus barbatus</i>	5.07	953	30y	$104.3 \times 10^5$	40°
	<b>Galliformes</b>					
200	<i>Lagopus lagopus</i>	0.524	268.36	18y	$18.81 \times 10^5$	40°
201	<i>Lagopus lagopus</i>	0.509	294.7	18y	$19.36 \times 10^5$	40°
202	<i>Callipepla gambelii</i>	0.126	65.21	10y	$2.38 \times 10^5$	40°
203	<i>Gallus gallus</i>	2.43	670.47	16y	$39.155 \times 10^5$	40°
	<b>Gruiformes</b>					
204	<i>Grus canadensis</i>	3.89	702.2	25y	$64 \times 10^5$	40°
205	<i>Anthropoides paradisea</i>	4.03	919.6	25y	$83.9 \times 10^5$	40°
206	<i>Crex crex</i>	0.096	68.13	15y	$3.75 \times 10^5$	40°
207	<i>Fulica atra</i>	0.412	176	20y	$12.85 \times 10^5$	40°
	<b>Psittaciformes</b>					
208	<i>Melopsittacus undulatus</i>	0.0337	41.38	15y	$2.265 \times 10^5$	40°
209	<i>Myiopsitta monachus</i>	0.0815	67.72	18y	$4.45 \times 10^5$	40°
210	<i>Myiopsitta monachus</i>	0.0831	68.13	18y	$4.47 \times 10^5$	40°
211	<i>Myiopsitta monachus</i>	0.0831	59	18y	$3.87 \times 10^5$	40°
212	<i>Neophema pulchella</i>	0.04	50.16	15y	$2.74 \times 10^5$	40°
	<b>Cuculiformes</b>					
213	<i>Cuculus canorus</i>	0.128	108.26	17y	$6.7 \times 10^5$	40°
214	<i>Eudynamis scolopacea</i>	0.188	142.12	17y	$8.8 \times 10^5$	40°
215	<i>Cacomantis variolosus</i>	0.0238	16.3	12y	$0.71 \times 10^5$	40°
216	<i>Cacomantis variolosus</i>	0.0238	10.45	12y	$0.46 \times 10^5$	40°
217	<i>Centropus senegalensis</i>	0.175	130	17y	$8.06 \times 10^5$	40°
	<b>Strigiformes</b>					
218	<i>Athene cunicularia</i>	0.1427	58.52	19y	$4.06 \times 10^5$	40°
219	<i>Glaucidium cuculoides</i>	0.163	74.82	20y	$5.46 \times 10^5$	40°
220	<i>Strix aluco</i>	0.52	179.74	25y	$16.4 \times 10^5$	40°
221	<i>Aegolius acadicus</i>	0.124	56.43	19y	$3.91 \times 10^5$	40°
222	<i>Asio otus</i>	0.240	110.35	22y	$8.86 \times 10^5$	40°
	<b>Caprimulgiformes</b>					
223	<i>Podargus ocellatus</i>	0.145	48.9	15y	$2.68 \times 10^5$	40°
224	<i>Chordeiles minor</i>	0.072	38	12y	$1.66 \times 10^5$	40°
225	<i>Caprimulgus europaeus</i>	0.0774	55.59	12y	$2.43 \times 10^5$	40°
226	<i>Phalaenoptilus nuttalli</i>	0.035	13.376	12y	$0.586 \times 10^5$	40°
227	<i>Eurostopus guttatus</i>	0.088	35.11	13y	$1.67 \times 10^5$	40°
	<b>Apodiformes</b>					
228	<i>Calypte anna</i>	0.0054	9.9	4y	$14.45 \times 10^3$	40°
229	<i>Eugenes fulgens</i>	0.0066	8.6	4y	$12.55 \times 10^3$	40°
230	<i>Calypte costae</i>	0.0032	4.476	4y	$6.5 \times 10^3$	40°
231	<i>Selasphorus platycercus</i>	0.003	5.79	4y	$8.85 \times 10^3$	40°
232	<i>Patagona gigas</i>	0.0191	24.74	8y	$72.24 \times 10^3$	40°
233	<i>Archilochus alexandri</i>	0.0033	6.27	4y	$9.15 \times 10^3$	40°
	<b>Coliiformes</b>					
234	<i>Colius striatus</i>	0.0512	46.8	12y	$2.0 \times 10^5$	40°

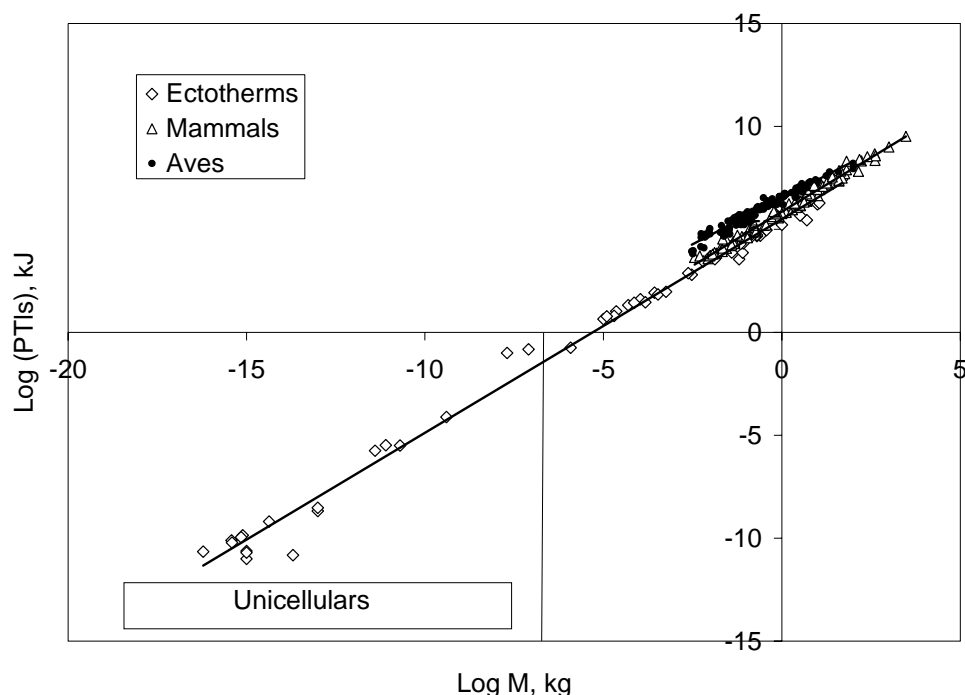


235	<i>Colius castanotus</i>	0.069	89.45	12y	$3.9 \times 10^3$	40°
236	<i>Colius castanotus</i>	0.0577	66	12y	$2.9 \times 10^3$	40°
237	<i>Urocolius macrourus</i>	0.0485	63.5	12y	$2.8 \times 10^3$	40°
238	<i>Urocolius indicus</i>	0.0535	61.86	12y	$2.7 \times 10^3$	40°
	<b>Trogoniformes</b>					
239	<i>Alcedo atthis</i>	0.0343	32.6	10y	$1.19 \times 10^3$	40°
240	<i>Trogon rufus</i>	0.053	37.2	12y	$1.6 \times 10^3$	40°
	<b>Coraciiformes</b>					
241	<i>Upupa epops</i>	0.067	47.65	12y	$2.08 \times 10^3$	40°
242	<i>Merops viridis</i>	0.0338	25.5	10y	$0.93 \times 10^3$	40°
243	<i>Merops viridis</i>	0.0338	33.86	10y	$1.2 \times 10^3$	40°
	<b>Piciformes</b>					
244	<i>Jynx torquilla</i>	0.0318	30.9	10y	$1.12 \times 10^3$	40°
245	<i>Dendrocopus major</i>	0.098	77.3	15y	$4.23 \times 10^3$	40°
246	<i>Picoides major</i>	0.117	89.87	15y	$4.92 \times 10^3$	40°
	<b>Passeriformes</b>					
247	<i>Regulus regulus</i>	0.0055	15.88	10.53y	$61 \times 10^3$	40°
248	<i>Psaltriparus minimus</i>	0.0055	10.45	10.53y	$40.16 \times 10^3$	40°
249	<i>Auriparus flaviceps</i>	0.0068	14.212	10.96y	$56.87 \times 10^3$	40°
250	<i>Tiaris canora</i>	0.0007	13.376	11.02y	$53.82 \times 10^3$	40°
251	<i>Parula americana</i>	0.007	10.45	11.02y	$42.05 \times 10^3$	40°
252	<i>Vermivora pinus</i>	0.0078	12.958	11.36y	$53.73 \times 10^3$	40°
253	<i>Loxops parva</i>	0.0079	12.122	11.37y	$50.3 \times 10^3$	40°
254	<i>Troglodytes troglodytes</i>	0.009	18.39	11.56y	$77.6 \times 10^3$	40°
255	<i>Troglodytes aedon</i>	0.0097	25.08	11.7y	$107.1 \times 10^3$	40°
256	<i>Dendroica dominica</i>	0.0098	13.794	11.75y	$59.16 \times 10^3$	40°
257	<i>Delichon irbica</i>	0.0205	30.51	13.5y	$150.34 \times 10^3$	40°
258	<i>Carduelis chloris</i>	0.0311	46.816	14.635y	$250 \times 10^3$	40°
259	<i>Cardinalis cardinalis</i>	0.0410	50.996	15.424y	$287.1 \times 10^3$	40°
260	<i>Pipilo alberti</i>	0.0466	62.7	15.61y	$361.68 \times 10^3$	40°
261	<i>Loxia pytyopsittacus</i>	0.0537	68.97	16.23y	$408.73 \times 10^3$	40°
262	<i>Perisoreus canadensis</i>	0.0645	83.6	16.81y	$512.94 \times 10^3$	40°
263	<i>Sturnus vulgaris</i>	0.067	75.66	26.93y	$467.6 \times 10^3$	40°
264	<i>Sturnus vulgaris</i>	0.075	71.33	17.3y	$488.3 \times 10^3$	40°
265	<i>Cyanocitta cristata</i>	0.0808	71.9	17.54y	$460.48 \times 10^3$	40°
266	<i>Cyanocitta stelleri</i>	0.0991	86.1	18.24y	$573.2 \times 10^3$	40°
267	<i>Acridotheres cristatellus</i>	0.1094	104.08	18.58y	$705.84 \times 10^3$	40°
268	<i>Pica pica</i>	0.202	148.4	20.88y	$1131 \times 10^3$	40°
269	<i>Corvus monedula</i>	0.215	161.35	21.13y	$1244 \times 10^3$	40°
270	<i>Corvus caurinus</i>	0.306	412.56	22.6y	$3403.2 \times 10^3$	40°
271	<i>Corvus frugilegus</i>	0.390	225.72	23.664y	$1950 \times 10^3$	40°
272	<i>Corvus brachyrhynchos</i>	0.3848	283.4	23.6y	$2441 \times 10^3$	40°
273	<i>Corvus corone</i>	0.518	286.33	24.975y	$2610 \times 10^3$	40°
274	<i>Corvus corone</i>	0.540	330.22	25.17y	$3034 \times 10^3$	40°
275	<i>Corvus corax</i>	0.85	384.56	27.44y	$3851 \times 10^3$	40°
276	<i>Corvus corax</i>	0.866	396.68	27.54y	$3988 \times 10^3$	40°
277	<i>Corvus corax</i>	1.203	475.27	29.31y	$5085 \times 10^3$	40°
278	<i>Corvus corax</i>	1.208	517.48	29.33y	$5540 \times 10^3$	40°

An allometric analysis has shown that a linear relationship between the total metabolic energy per lifespan ( $P_{ls} = PT_{ls}$ , kJ) and the body mass ( $M$ , kg) of all together - Ectotherms, Mammals and Aves ( $n=278$  individuals) in log-log plot holds:

$$PT_{ls} = A^{all}_{ls} M^{1.0787 \pm 0.11} \quad (8)$$

with corresponding coefficient  $R^2=0.980$ , coefficient  $A^{all}_{ls} = 15.18 \times 10^5$  kJ/kg, standard error of the exponent  $SE = \pm 0.11$  and confidence interval ( $CI$ ) of 95% (0.968-1.188). The graphic presentation of relationship (8) for all 278 Ectotherms, Mammals and Aves is shown on **Fig. 1**.



**Fig. 1.** The relationship between the total metabolic energy per lifespan (Pls=PTIs, kJ) and the body mass (M, kg) for 278 Ectotherms, Mammals and Aves. The unicellular organisms are divided from multicellular organisms (animals) by vertical line.

The relationship for Ectotherms, Mammals and Aves ( $n=260$ ) without Protozoa is linear too:

$$PT_{ls} = A_{ls} M^{1.0089 \pm 0.042} \quad (9)$$

with  $R^2=0.897$ , coefficient  $A_{ls}=14.16 \times 10^5$  kJ/kg, standard error of the exponent  $SE = \pm 0.042$  and  $CI$  of 95% (0.967-1.051). In (8) and (9), the linear coefficients  $A_{ls}$  vary negligible and appears to be the total metabolic energy, exhausted during the lifespan per 1kg body mass of animals.

In (8), for all 278 Ectotherms, Mammals and Aves and in (9) for all animals without Protozoa, the value of the exponent is equal to 1.0 in the confidence interval of 95%. The high correlation coefficients ( $R^2=0.897-0.980$ ) between the total metabolic energy per lifespan and the body mass of animals means that the correlations are not random.

The relationships between the total metabolic energy per lifespan and the body mass separately for Ectotherms, Mammals and Aves are given in **Table 2**.

It is well known fact that the log-log plot reduces the residual variability, which means

that large deviations from predicted, appear as small deviations. In (8) and (9) the down limits

of confidence intervals of the exponents are equal (0.967-0.968), but the upper limits are different ( $r=1.051$  without Protozoa and 1.188 with Protozoa), because the total metabolic energy per lifespan for Protozoa scale with body mass as  $M^{1.16}$  ( $R^2=0.95$ ).

In this connection, P-level of the correlation (8) has been estimated by Student's t-test for  $p=0.00001$  and two null hypotheses for exponents and intercepts were tested for Ectotherms, Mammals and Aves using method of analyses of covariance ANCOVA.

Since, the histogram of residual total metabolic energy per lifespan  $P_{ls}$  against body mass  $M$  for all 278 Ectotherms, Mammals and Aves individuals shows the normal (Gaussian) distribution, this means that the general relationship (8) is statistically significant for  $p=0.00001$ .

The first tested hypotheses is that the slopes of exponents of the regression lines for Ectotherms and Mammals are all the same. The 95% confidence interval of the slopes ( $r=1.038 \pm 0.024$ ) for Ectotherms is 1.014-1.062

and for Mammals ( $r=1.051\pm 0.029$ ) is 1.022-1.080. Since the confidence intervals of the slopes for Ectotherms and Mammals are overlap the first hypothesis for Ectotherms and Mammals is confirmed.

The second tested hypothesis is that the intercepts of the regression for Ectotherms and Mammals are all the same. The confidence intervals (95% level) of the intercepts for Ectotherms are 5.31-5.69 and the same for Mammals is 5.81-5.88. Since the two intercepts are different the second hypothesis is rejected. Consequently, the Ectotherms and Mammals appear on general relationship (8) as two groups with equal slope but different intercept.

The same hypotheses applied for Aves against Ectotherms and Mammals show that the 95% confidence interval of the slopes ( $r=0.893\pm 0.033$ ) for Aves is 0.86-0.926 and the confidence intervals (95% level) of the intercept for Aves is 6.41-6.73. Therefore, the

confidence interval of the slope and intercept for Aves differs considerably from the confidence interval of slopes and intercepts for Ectotherms and Mammals. This shows that three groups (Ectotherms, Mammals and Aves) clearly distinguish on the general relationship (8). In spite of the fact that the group of Aves differ considerably from the groups of Ectotherms and Mammals, because of small range of variation ( $1\times 10^5$  times) between body mass of Aves in comparison to big range of variation ( $3\times 10^{21}$  times) between body mass of all individuals (Ectotherms, Mammals and Aves) the group of Aves affect negligible the slope of general relationships (8).

### DISCUSSION

Some relationships between the total metabolic energy per lifespan and the body mass, separately for class Ectotherms, Mammals and Aves, and in combination of all are summarized in **Table 2**.

**Table 2.** The relationships between the total metabolic energy per lifespan (Pls, kJ) and the body mass (M, kg) for class Ectotherms, Mammals and Aves, separately and in combination (n- is the number of individuals).

Item	Class of animals	Pls = $AIsM^r$	$R^2$
a)	All(Ectotherms, Mammals and Aves)(n=278)	Pls = $15.18 \times 10^5 M^{1.0787 \pm 0.11}$	0.980
b)	All without Protozoa (n=260)	Pls = $14.16 \times 10^5 M^{1.0089 \pm 0.042}$	0.897
c)	Ectotherms (n=56)	Pls = $3.14 \times 10^5 M^{1.038 \pm 0.024}$	0.992
d)	Mammals (n=95)	Pls = $7.15 \times 10^5 M^{1.051 \pm 0.029}$	0.981
e)	Ectotherms and Mammals (n=151)	Pls = $5.88 \times 10^5 M^{1.062 \pm 0.030}$	0.994
f)	Ectotherms without Protozoa (n=38)	Pls = $2.268 \times 10^5 M^{0.958 \pm 0.035}$	0.988
g)	Aves (n=127)	Pls = $32.2 \times 10^5 M^{0.893 \pm 0.033}$	0.957
h)	Aves and Mammals(n=222)	Pls = $17.3 \times 10^5 M^{0.896 \pm 0.036}$	0.886
i)	Aves and Ectotherms (n=183)	Pls = $25.77 \times 10^5 M^{1.106 \pm 0.12}$	0.984

**Table 2** shows that in five equations (a, b, c, d, e) – (a) for all Ectotherms, Mammals and Aves, (b) for all animals without Protozoa, separately for Ectotherms(c) and Mammals(d), and for the combination Ectotherms – Mammals(e), the exponent  $r$  falls in the interval of 1.0-1.08. In the three equations (f, g, h) – (f) for Ectotherms without Protozoa, (g) for Aves and (h) for the combination Aves-Mammals, the exponent  $r$  is lower than 1.0 and falls in the interval of  $r=0.893-0.896$ . In the combination (i) for Aves- Ectotherms, the exponent  $r$  exceeds 1.08 ( $r=1.106$ ). It is observed that exponents for class Aves, combinations between Aves-Mammals and combination between Aves-Ectotherms define the minimum and the maximum limits of the exponent  $r$ , from the minimum of 0.893 to the

maximum of 1.106. The mean point of this interval (0.893-1.106) is the value 0.999 that is close to 1.0. All animals (Ectotherms, Mammals and Aves), without Protozoa, give the relationship with exponent exactly 1.0 i.e.  $r=1.0089$  with standard error of the slope  $SE=\pm 0.042$ . In the case of all animals (Ectotherms, Mammals and Aves), including Protozoa, the exponent becomes 1.0787 with standard error of the slope  $SE= \pm 0.11$ . This show, that Protozoa enlarges considerably the exponent from 1.0089 to 1.0787 and the standard error of the slope from 0.042 to 0.11. This is possible, because the Ectotherms, including Protozoa, have the biggest range of body mass ( $1\times 10^{17}$  times) in comparison to Mammals ( $1\times 10^7$  times), and to Aves ( $1\times 10^5$  times). Without Protozoa, the Ectotherms have

again a higher range of body mass, about  $5 \times 10^7$  times, in comparison to Mammals and to Aves ( $1 \times 10^7$  times). The Ectotherms only, including Protozoa, have exponent  $r = 1.038$ , but without Protozoa the exponent is  $r = 0.958$ . The mean point (0.996) of this interval (from 0.958 to 1.038) is very close to 1.0. Thus, in other combinations between Ectotherms, Mammals and Aves, the exponent  $r$  varied around 1.0 and does not exceed the given minimum and maximum values (from 0.893 to 1.106) with mean point close to 1.0.

From eq. 'c', 'd', 'g' on Table 2 can be observed that the total metabolic energy per lifespan, per 1 kg body mass ( $A_{ls}$ ) grows from the value of  $3.14 \times 10^5$  kJ/kg in Ectotherms to  $7.15 \times 10^5$  kJ/kg in Mammals, and to  $32.2 \times 10^5$  kJ/kg in Aves. Thus,  $A_{ls}$  rises 10 times only from Ectotherms to Aves, despite of the 21 orders of magnitude difference between the body mass of animals. This shows that in evolution the coefficient  $A_{ls}$  is a relatively constant parameter. On the contrary, the individual values of  $A_{ls}$  between 278 studied organisms change 300-500 times. For example: from Bacteria to *Elephas maximum* it changes about 300 times and from Bacteria to *Covus corax* it changes about 550 times (see Appendices).

The linearity between the total metabolic energy per lifespan and the body mass of animals leads to additive connection between three allometric relationships: 1/ the basal metabolic rate and the body mass ( $P = aM^k$ ), 2/ the lifespan and the body mass ( $T_{ls} = bM^n$ ) and 3/ the total metabolic energy per lifespan and the body mass ( $P_{ls} = A_{ls}M^r$ ). The additive connection can be expressed by the equations (10) and (11):

$$P_{ls} = PT_{ls} = (aM^k) \times (bM^n) = abM^{k+n} = A_{ls}M^r \quad (10)$$

$$A_{ls} = ab, \quad r = k+n = 1.0 \quad (11)$$

If we know the 'metabolism-mass' or the 'lifespan-mass' relationship, we can calculate the other additive relationship, using equations (10) and (11).

A several other scientific problems are connected with total metabolic energy per lifespan. However, the finding of the basic scaling laws in biology and others natural sciences will allow us to build 'scientific theory of all'.

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