Journal of Animal and Veterinary Advances 7 (4): 425-432, 2008
ISSN: 1680-5593

The Near to Linear Allometric Relationship Between the Total Metabolic Energy per Life Span and the Body Mass of Aves

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Abstract: The aim of this study is to establish and calculate the allometric relationship between the total metabolic energy per life span and the body mass in Passerine and Nonpasserine birds for maximum and life span in captivity. The study shows that it exists near to linear relationship between the total metabolic energy per life span PTls (kJ) and the body mass M (kg) of birds from the type: $PT_{ls}= A^0_{ls}M^k$, where P (kJ day^{-1}) is the basal metabolic rate, Tls (day) is the life span (maximum or life span in captivity) and A^0_{ls} (kJ kg^{-1}) is the total metabolic energy, exhausted during the life span per 1 kg body mass of birds. The received results show that for all birds, the power coefficient (k) in the 'lifespan metabolism-mass' relationship fall in the interval 0.8776-0.934 (for maximum and life span in captivity). For maximum life span the power coefficient k for all birds is 0.904 ($R^2 = 0.976$) and separately for Passerine it is 0.935 ($R^2 = 0.987$), for Nonpasserine it is 0.926 ($R^2 = 0.98$). The linear coefficient A^0_{ls} for all birds is 26.866×10^5 kJ kg^{-1} and separately for Passerine it is $36,728\times10^5$ kJ kg^{-1}, for Nonpasserine it is 25.199×10^5 kJ kg^{-1} . Possibly, the linearity between lifespan metabolic energy and body mass expresses a general allometric law in animal energetics, since it is valid for Poikilothetms, Mammals and approximately for Aves.

Key words: Aves, basal metabolic rate, lifespan, total metabolic energy

INTRODUCTION

The patterns existing between the other fundamental characters of living organisms and their body mass are generally described as a power function. The bioenergetic studies on Aves (Hemmingsen, 1960; Kleiber, 1961; Schmidt-Nielsen, 1984) have shown that the basal metabolic rate (P) in birds is related to the body mass (M) as expressed by the equation of type $P = aM^k$, where a and k are allometric parameters.

Lasiewski and Dawson (1967) divide the birds into 2 big groups, respectively basal metabolic rate: Passeriformes (with higher metabolic rate) and Nonpasseriformes (with smaller metabolic rate). Lasiewski and Dawson have found that for all birds the basal metabolic rate (P, $kcald^{-1}$) is related to the body mass (M, kg) as $P = 86.4M^{0.668}$, separately for Passerine as $P = 129M^{0.724}$ and for Nonpasserine as $P = 78.3M^{0.723}$.

On the contrary, Rezende *et al.* (2002) analyzed and compared the scaling of basal and maximal thermogenic metabolic rates in Passerine and Nonpasserine birds using conventional and phylogenetic methods. They found no statistical differences in the scaling of avian (Passerine and Nonpasserine) energetics.

Aschoff and Pohl (1970a, b) divide the birds into duirnal and nocturnal, respectively basal metabolic rate too. If the period of the normal activity of the birds is signed by ρ and period of relaxation is signed by α, Aschoff and Pohl for Passerine birds have received $P_\alpha = 140.9M^{0.704}$ and $P_\rho = 114.8M^{0.726}$. For Nonpasserine birds have received $P_\alpha = 91.0M^{0.729}$ and $P_\rho = 73.5M^{0.734}$, respectively (where P in kcal d^{-1}; M in kg).

Bennett and Harvey (1987) have received that the basal metabolic rate in all birds is proportional to body surface i.e. power coefficient k in 'metabolism-mass' relationship is near to 0.67.

Speakman (2005) have analysed data for basal metabolic rate in birds and have received the same result. The 'metabolism-mass' relationship for all birds is from the type $P = 3.4M^{0.671}$ with $R^2= 0.958$ (where P in kJ d^{-1} and M in g). The power coefficient 0.671 showed that the basal metabolism is propotional to body surface.

Nagy (1987, 2005) measuring field metabolic rate in birds using the doubly labeled water method have received the similar power coefficient, but 3-fold higher linear coefficient $P = 10.5M^{0.681}$ with $R^2 = 0.938$ (where P in kJ d^{-1}; M in g).

Hinds *et al*. (1993) have measured the minimum and maximum metabolism in response to cold in birds. For minimum metabolism these authors have received the 'metabolism-mass' relationship with power coefficient 0.646 ($R^2 = 0.979$) and for maximum metabolism with power coefficient 0.615 ($R^2 = 0.987$), respectively. These power coefficients are significally lower than 0.67.

McKechnie *et al*. (2006) show that there is a phenotypic plasticity in the scaling of avian basal metabolic rate and this phenotypic plasticity is a major contributor to avian inter-specific metabolic variation. The authors used a generalized least-squares approach, using the phylogeny to account for covariance among the species and have demonstrated that power coefficients in 'metabolism-mass' relationships for Aves is 0.623. The scaling exponent related to the basal metabolic rate to body mass in captive-raised birds (0.670) was significantly shallower than in wild-caught birds (0.744).

Ronning *et al*. (2005) have received that intraspecific scaling exponents for zebra finch (*Taeniopygia guttata*) are in interval 0.58-0.7440 for males and 0.669-0.899 for females. These data are lower than the intraspecific scaling reported for birds, which in some cases exceeds 1.0. For example, Kvist and Lindström (2001) have shown that the power coefficient in 'metabolism-mass' relationships for migratory waders have intra-individuals, intraspecific, interspecific and seasonal variations and in some cases intraspecific scaling exceeds 1.0.

The main aims of the studies on bird's metabolism, in scientific publications consists of specifying the allometric slopes of 'metabolism-mass' relationships. But despite all, the results for these relationship remain controversial, as the variations of power coefficient for basal metabolic rate in other life conditions are in wide interval, from about 0.6-0.9 and over. This problem is valid for Poikilotherms and Mammals too and is well discussed in 'Metabolic scaling: consensus or controversy' (Agutter and Wheatley, 2004).

In previous researches Atanasov (2005a, b; 2007) showed that for Poikilotherms and Mammals the relationships between the total metabolic energy per life span ($P_{1s} = PT_{1s}$) and body mass (M) over a broad number of animals is expressed by the linear equation of the type $P_{1s} = A_{1s}M$ (where P is the basal metabolic rate and A_{1s} is linear coefficient).

Since, the basal metabolic rate of birds is proportional to body mass with power coefficient in interval 0.58-0.9 and the life span of birds is proportional to body mass with power coefficient in interval 0.19-0.216 (Lindstedt and Calder, 1976; Speakman, 2005), the product $P_{1s} = PT_{1s}$ will be proportional to body mass with power coefficient in very wide interval 0.77-1.12.

The aim of this study is to establish and calculate the allometric relationship between the total metabolic energy per life span and the body mass in Passeriformes and Nonpasseriformes birds for maximum and life span in captivity and estimate the linearity of this relationship.

MATERIALS AND METHODS

The study involves 127 Aves species: 95 species from 23 Nonpasseriformes orders (*Struthioniformes*, *Rheiformes*, *Casuariiformes*, *Apterygiformes*, *Sphenisciformes*, *Procellariiformes*, *Pelecaniformes*, *Ciconiiformes*, *Anseriformes*, *Charadriiformes*, *Columbiformes*, *Falconiformes*, *Galliformes*, *Gruiformes*, *Psittaciformes*, *Cuculiformes*, *Strigiformes*, *Caprimulgiformes*, *Apodiformes*, *Coliiformes*, *Trogoniformes*, *Coraciiformes*, *Piciformes*) and 32 species from order Passeriformes.

The data for the body mass (M) and the basal metabolic rate (P) of these birds were collected from review paper of Bennett and Harvey (1987).

We estimate the slope of relationship between the total metabolic energy per life span and body mass in 2 cases-for maximum life span and for life span in captivity.

The maximum life span (T_{1s}) of birds were calculated using the relationship (formula) between body mass (M) and life span in birds received from Speakman (2005):

1 $T_{1s} = 20.2\ M^{0.216}$ (where T_{1s} is in years and M is in kg).

The life span in captivity (T_{1sc}) were calculated using the formula of Lindstedt and Calder (1976) :

2 $T_{1sc} = 28.3\ M^{0.19}$ (where T_{1sc} is in years and M is in kg).

For each bird the total metabolic energy per life span (P_{1s} and P_{1sc}) were calculated as a product from the basal metabolic rate P (kJ d^{-1}) and T_{1s} (d) or T_{1sc} (d) life span:

3 P_{1s} (kJ) = P (kJ d^{-1})$\times T_{1s}$ (d) and P_{1sc} (kJ) = P (kJ d^{-1}) $\times$ T_{1sc} (d)

For each bird the total metabolic energy per life span, per 1kg body mass were calculated as a ratio between P_{1s} (kJ) or P_{1sc} (kJ) and the body mass M (kg) of birds:

4 A_{1s} (kJ kg^{-1}) = (PT_{1s}) /M and A_{1sc} (kJ kg^{-1}) = (PT_{1sc}) /M

RESULTS AND DISCUSSION

Table 1 contains data for 23 orders with 95 Nonpasserine birds and 1 orders with 32 Passerine birds.

Table 1: Data for the body mass M, basal metabolic rate P , life span T_{ls}*, and calculated data for the total metabolic energy per life span PT_{ls}** for 127 birds

AVES	M (kg)	P (kJ d^{-1})	T_{ls} (y)*	Pt_{ls} (kJ)**
Order Struthioniformes				
1. Struthio camelus	100	9823	54.6 (67.9)	195.7×10^{6} (243.4×10^{6})
2. Struthio camelus	100	5442,36	54.6 (67.9)	108.5×10^{6} (134.9×10^{6})
Order Rheiformes				
3. Rhea americana	21.7	3344	39.27 (50.8)	47.962x 10^{6} (62×10^{6})
Orger Casuariiformes				
4. Casuarius bennetti	17.6	2156.9	37.5 (48.8)	29.510^{6} (38.4×10^{6})
5.Dromaius novaehollandiae	38.925	3746.1	44.55 (56.7)	60.9×10^{6} (77.5×10^{6})
Order Apterygiformes				
6.Apteryx australis	2.38	347.77	24.36 (33.4)	30.9×10^{5} (42.4×10^{5})
7.Apteryx owenii	1.095	178.486	20.6 (28.8)	13.4×10^{5} (18.7×10^{5})
8.Aptreryx haasti	2.54	360.734	24.7 (33.8)	32.5×10^{5} (44.5×10^{5})
Order Sphenisciformes				
9.Pygoscelis papua	6.29	1603.45	30 (40)	17.5×10^{6} (23.4×10^{6})
10.Pygoscelis adeliae	3.97	1055.87	27.2 (36.8)	10.48×10^{6} (14.18×10^{6})
11.Eudyptes pachyrhynchus	2.6	597.32	24.8 (34)	54.07×10^{5} (74.1×10^{5})
12.Eudyptes crestatus	2.506	862	24.6 (33.7)	77.4×10^{5} (106×10^{5})
13.Eudyptes crestatus	2.33	503.7	24.2 (33)	44.5×10^{5} (60.67×10^{5})
14.Eudyptula albosignata	1.15	570.57	20.82 (29)	43.36×10^{5} (60.4×10^{5})
Order Procellariiformes				
15.Macronectus giganteus	3.63	1492.68	26.7 (36)	14.5×10^{6} (16×10^{6})
16.Pterodroma hypoleuca	0.18	89.87	13.9 (20.4)	4.56×10^{5} (6.7×10^{5})
17.Pterodroma mollis	0.274	150.9	15.3 (22)	8.43×10^{5} (12.3×10^{5})
18.Pachyptila salvini	0.165	133.76	13.7 (20)	6.69×10^{5} (9.76×10^{5})
19.Puffinus griseus	0.740	249.13	18.9 (26.7)	17.18×10^{5} (24.3×10^{5})
Order Pelecaniformes				
20.Pelecanus occidentalis	3.038	894.5	25.67 (35)	83.8×10^{5} (114.27×10^{5})
21.Sula dactylatra	1.289	475.26	21.3 (29.7)	36.95×10^{5} (51.68×10^{5})
22.Phalacrocorax auritus	1.33	474	21.5 (29.9)	37.2×10^{5} (50.2×10^{5})
23.Sula sula	1.017	375.78	20.3 (28.4)	27.8×10^{5} (38.9×10^{5})
Order Ciconiiformes				
24.Ardea herodias	1.87	535	23.1 (31.9)	45.1×10^{5} (62.2×10^{5})
25.Hydranassa tricolor	0.31	147.55	15.7 (22.6)	1×10^{6} (12.2×10^{5})
26.Mysteria americana	2.5	840.18	24.6 (33.7)	75.44×10^{5} (103.3×10^{5})
27.Leptoptilos javanicus	5.71	1283.2	29.4 (39.4)	13.77×10^{6} (184.55×10^{5})
Order Anseriformes				
28.Cygnus biccinator	8.88	1747.24	32.4 (43)	206.6×10^{5} (274×10^{5})
29.Branta bernicla	1.168	390.4	20.9 (29)	29.8×10^{5} (41.3×10^{5})
30.Aix sponsa	0.485	271.7	17.3 (24.7)	17.15×10^{5} (24.4×10^{5})
31.Anas platyrhynchos	1.132	434.7	20.7 (29)	32.8×10^{5} (46×10^{5})
32.Anas crecca	0.25	143.8	15 (21.7)	7.87×10^{5} (11.4×10^{5})
33.Anas querquedula	0.289	192.7	15.4 (22.3)	10.83×10^{5} (15.7×10^{5})
Order Charadriiformes				
34.Tringa ochropus	0.09	79.4	12 (18)	3.477×10^{5} (5.2×10^{5})
35.Catharacta skua	0.97	409.6	20 (28)	29.9×10^{5} (41.86×10^{5})
36.Larus delawarensis	0.439	249.13	16.9 (24)	15.37×10^{5} (21.8×10^{5})
37.Larus occidentalis	0.761	293	19 (26)	20.3×10^{5} (27.8×10^{5})
38.Gygis alba	0.0981	70.22	12.2 (18)	3.13×10^{5} (4.61×10^{5})
Order Columbiformes				
39.Columba unicincta	0.318	148	15.8 (23)	8.5×10^{5} (12.42×10^{5})
40.Columba livia	0.314	145.46	15.7 (23)	8.33×10^{5} (12.21×10^{5})
41.Columba livia	0.266	140.87	15.1 (22)	7.76×10^{5} (11.3×10^{5})
42.Streptopelia decaocto	0.187	110	14 (20)	5.6×10^{5} (8.03×10^{5})
43.Aythya fuligula	0.574	233.2	17.9 (25)	15.2×10^{5} (21.28×10^{5})
Order Falconiformes				
44.Vultur gryphus	10.32	1467.18	33.4 (44)	17.9×10^{5} (23.56×10^{6})
45.Falco sparverius	0.117	72.73	12.8 (18)	3.37×10^{5} (4.78×10^{5})
46.Accipiter nisus	0.135	81.93	13.1 (19)	3.92×10^{5} (5.68×10^{5})
47.Buteo buteo	1.012	324.37	20.25 (28)	23.97×10^{5} (33.15×10^{5})
48.Gypaetus berbatus	5.07	953	28.7 (38)	99.8×10^{5} (132.18×10^{5})
Order Galliformes				
49.Lagopus lagopus	0.524	268.36	17.6 (25)	17.2×10^{5} (24.49×10^{5})
50. Lagopus lagopus	0.509	294.7	17.46 (25)	18.78×10^{5} (26.9×10^{5})
51.Lophortyx gambelii	0.126	65.21	12.9 (19)	3.07×10^{5} (4.5×10^{5})
52.Gallus gallus	2.43	670.47	25.5 (33)	60×10^{5} (80.76×10^{5})
Order Gruiformes				
53.Grus canadensis	3.89	702.2	27.1 (36)	69.45×10^{5} (92.27×10^{5})
54.Anthropoides paradisea	4.03	919.6	27.3 (37)	91.6×10^{5} (124.2×10^{5})

Tabe 1: Continue

AVES	M (kg)	P (kJ d^{-1})	T_{ls} (y)*	Pt_{ls} (kJ)**
55.Crex crex	0.096	68.13	12.2 (18)	3.03×10^{5} (4.47×10^{5})
56.Fulica atra	0.412	176	16.67 (24)	10.7×10^{5} (15.4×10^{5})
Order Psittaciformes				
57.Melopsittacus undulatus	0.0337	41.38	9.7 (15)	1.465×10^{5} (2.265×10^{5})
58.Myiopsitta monachus	0.0815	67.72	11.75 (17)	2.9×10^{5} (4.2×10^{5})
59. Myiopsitta monachus	0.0831	68.13	11.8 (17)	2.93×10^{5} (4.23×10^{5})
60 Myiopsitta monachus	0.0831	59	11.8 (17)	2.54×10^{5} (3.66×10^{5})
61.Neophema pulchella	0.04	50.16	10 (15)	1.83×10^{5} (2.75×10^{5})
Order Cuculiformes				
62.Cuculus canorus	0.128	108.26	13 (19)	5.14×10^{5} (7.5×10^{5})
63.Eudyramys scolopacea	0.188	142.12	14.1 (21)	7.31×10^{5} (10.9×10^{5})
64.Cacomantis variolosus	0.0238	16.3	9 (14)	53.5×10^{3} (83.3×10^{3})
65.Cacomantis variolosus	0.0238	10.45	9 (14)	34.3×10^{3} (53.4×10^{3})
66.Centropus senegalensis	0.175	130	13.9 (20)	6.6×10^{5} (9.49×10^{5})
Order Strigiformes				
67.Speotyto cunicularia	0.1427	58,52	13.3 (19)	2.84×10^{5} (4.06×10^{5})
68.Glaucidium cuculoides	0.163	74.82	13.65 (20)	3.73×10^{5} (5.46×10^{5})
69.Strix aluco	0.52	179.74	17.5 (25)	11.5×10^{5} (16.4×10^{5})
70.Aegolius acadicus	0.124	56.43	12.9 (19)	2.66×10^{5} (3.91×10^{5})
71.Asio otus	0.240	110.35	14.8 (22)	5.96×10^{5} (8.86×10^{5})
Order Caprimulgiformes				
72.Podargus ocellatus	0.145	48.9	13.3 (20)	2.374×10^{5} (3.57×10^{5})
73.Chordeiles minor	0.072	38	11.4 (17)	1.58×10^{5} (2.35×10^{5})
74.Caprimulgus europaeus	0.0774	55.59	11.6 (17)	2.35×10^{5} (3.45×10^{5})
75.Phalaenoptilus nuttalli	0.035	13.376	9.8 (15)	47.8×10^{3} (73.2×10^{3})
76.Eurostopodus guttatus	0.088	35.11	11.95 (18)	1.53×10^{5} (2.3×10^{5})
Order Apodiformes				
77.Calypte anna	0.0054	9.9	6.5 (10)	23.5×10^{3} (36.1×10^{3})
78.Eugenes fulgens	0.0066	8,77	6.8 (11)	21.7×10^{3} (35.2×10^{3})
79.Calypte costae	0.0032	4.476	5.8 (9)	9.47×10^{3} (14.7×10^{3})
80.Selasphorus platycercus	0.0038	5.85	6.06 (10)	12.9×10^{3} (21.35×10^{3})
81.Patagona gigas	0.0191	24.66	8.6 (13)	77.4×10^{3} (117×10^{3})
82.Archilochus alexandri	0.0033	5.43	5.88 (9)	11.65×10^{3} (17.8×10^{3})
Order Coliiformes				
83.Colius striatus	0.0512	46.8	10.6 (16)	1.81×10^{5} (2.733×10^{5})
84.Colius castanotus	0.069	89.45	11.3 (17)	3.69×10^{5} (5.55×10^{5})
85.Colius castanotus	0.0577	66	10.9 (16.4)	2.63×10^{5} (3.95×10^{5})
86.Colius macrourus	0.0485	63.5	10.4 (16)	2.41×10^{5} (3.708×10^{5})
87.Colius indicus	0.0535	61.86	10.7 (16.2)	2.42×10^{5} (3.658×10^{5})
Order Trogoniformes				
88.Trogon rufus	0.053	37.2	10.7 (16.2)	1.45×10^{5} (2.20×10^{5})
Order Coraciiformes				
89.Alcedo atthis	0.0343	32.6	9.75 (15)	1.16×10^{5} (1.785×10^{5})
90.Upupa epops	0.067	47.65	11.2 (16.9)	1.95×10^{5} (2.94×10^{5})
91.Merops viridis	0.0338	25.5	9.7 (15.2)	0.903×10^{5} (1.415×10^{5})
92.Merops viridis	0.0338	33.86	9.7 (15.2)	1.2×10^{5} (1.878×10^{5})
Order Piciformes				
93.Jynx torquilla	0.0318	30.9	9.6 (14.7)	1.08×10^{5} (1.658×10^{5})
94.Picoides major	0.098	77.3	12.2 (18.2)	3.44×10^{5} (5.315×10^{5})
95.Picoides major	0.117	89.87	12.7 (18.8)	4.166×10^{5} (6.162×10^{5})
Order Passeriformes				
96.Regulus regulus	0.0055	15.88	6.56 (10.53)	38×10^{3} (61×10^{3})
97.Psaltriparus minimus	0.0055	10.45	6.56 (10.53)	25×10^{3} (40.16×10^{3})
98.Auriparus flaviceps	0.0068	14.212	6.87 (10.96)	35.6×10^{3} (56.87×10^{3})
99.Tiaris canora	0.007	13.376	6.87 (11.02)	33.5×10^{3} (53.82×10^{3})
100.Parula americana	0.007	10.45	6.87 (11.02)	26.2×10^{3} (42.05×10^{3})
101. Vermivora pinus	0.0078	12.958	7.08 (11.36)	33.5×10^{3} (53.73×10^{3})
102.Loxops parva	0.0079	12.122	7.08 (11.37)	31.3×10^{3} (50.3×10^{3})
103.Troglodytes troglodytes	0.009	18.39	7.3 (11.56)	49×10^{3} (77.6×10^{3})
104.Troglodytes aedon	0.0097	25.08	7.4 (11.7)	67.7×10^{3} (107.1×10^{3})
105.Dendroica dominica	0.0098	13.794	7.4 (11.75)	37.2×10^{3} (59.16×10^{3})
106.Delichon irbica	0.0205	30.51	8.7 (13.5)	96.9×10^{3} (150.34×10^{3})
107.Carduelis chloris	0.0311	46.816	9.5 (14.635)	162.3×10^{3} (250.08×10^{3})
108.Cardinalis cardinalis	0.0410	50.996	10.1 (15.424)	188×10^{3} (287.1×10^{3})
109.Pipilo alberti	0.0466	62.7	10.4 (15.61)	238×10^{3} (361.68×10^{3})
110.Loxia pytyopsittacus	0.0537	68.97	10.7 (16.23)	269×10^{3} (408.73×10^{3})
111.Perisoreus canadensis	0.0645	83.6	11.2 (16.81)	341.7×10^{3} (512.94×10^{3})
112.Sturnus vulgaris	0.067	75.66	11.27 (16.93)	311.2×10^{3} (467.6×10^{3})
113.Sturnus vulgaris	0.075	77.33	11.5 (17.3)	324.6×10^{3} (488.3×10^{3})

Table 1: Continue

AVES	M (kg)	P (kJ d^{-1})	T_{ls} (y)*	Pt_{ls} (kJ)**
114.Cyanocitta cristata	0.0808	71.9	11.7 (17.54)	307×10^3 (460.48×10^3)
115.Cyanocitta stelleri	0.0991	86.1	12.3 (18.24)	386.5×10^3 (573.2×10^3)
116.Acridotheres cristatellus	0.1094	104.08	12.5 (18.58)	474.8×10^3 (705.84×10^3)
117.Pica pica	0.202	148.4	14.9 (20.88)	774.5×10^3 (1131×10^3)
118.Corvus monedula	0.215	161.35	14.5 (21.13)	854×10^3 (1244.5×10^3)
119.Corvus caurinus	0.306	412.56	15.6 (22.6)	23.5×10^5 (3403.2×10^3)
120.Corvus frugilegus	0.390	225.72	16.5 (23.664)	13.6×10^5 (1950×10^3)
121.Corvus brachyrhynchos	0.3848	283.4	16.4 (23.6)	16.96×10^5 (2441×10^3)
122.Corvus corone	0.518	286.33	17.5 (24.975)	18.3×10^5 (2610×10^3)
123. Corvus corone	0.540	330.22	17.7 (25.17)	21.33×10^5 (3034×10^3)
124. Corvus corax	0.850	384.56	19.5 (27.44)	27.4×10^5 (3851.5×10^3)
125. Corvus corax	0.866	396.68	19.6 (27.54)	28.4×10^5 (3987.5×10^3)
126. Corvus corax	1.203	475.27	21 (29.31)	36.4×10^5 (5084.7×10^3)
127. Corvus corax	1.208	517.48	21 (29.33)	39.66×10^5 (5539.8×10^3)

*The data for the life span in captivity are given in brackets; **The calculated total metabolic energy per life span in captivity is given in brackets

For Nonpasserine birds, the lowest body mass in the data set given in Table 1 is about 3×10^3 kg^{-1} in order Apodiformes and the highest body mass is 1×10^2 kg^{-1} in order Struthioniformes. This is the range of variation about 1×10^5 times. For Passerine birds the lowest body mass is about $5.5\times10^{\ 3}$ kg^{-1} in *Regulus regulus* and the highest body mass is 1.208 kg in *Corvus corax*. This is the range of variation of 2×10^2 times.

The lowest basal metabolic rate in the data set given in Table 1 is 4.4 kJ d^{-1} in $3.2\times10^{\ 3}$ kg^{-1} Calypte costae and the highest is 9.8×10^3 kJ d^{-1} in 100 kg Struthio camelus. This is a range of variation of over 1×10^4 times.

The lowest life span is about 5 years in order Apodiformes and the highest life span is about 55 years in order Struthioniformes. This is a range of variation of about 10 times.

The lowest total metabolic energy per life span is 2×10 kJ kJ^{-4} in order Apodiformes and the highest is 2×10^8 kJ^{-8} in order Struthioniformes. This is a range of variation of about 1×10 $times^{-4}$.

For maximum life span the graphic relationship between log (PT_{1s}) and log (M) for all 127 (Passerine and Nonpasserine) birds, is presented in Fig. 1.

Allometric analysis have shown that a near to linear relationship between the total metabolic energy per maximum life span and the body mass of birds in log-log plot holds:

5 $\log(PT_{1s}) = 6.4292 + 0.9037 \log M$, with $R^2 = 0.9767$

The above equation could be presented as:

6 $PT_{1s} = A^0_{1s} M^{0.9037}$ with linear coefficient $A^0_{1s} = 26.866\times10$ kJ kg^{-1} .

The high correlation coefficient 0.9767 between log (PT_{1s})-log (M) means that the correlation is not random and it indicates that about 98% of the variation in log (PT_{1s}) is due to variation in log (M).

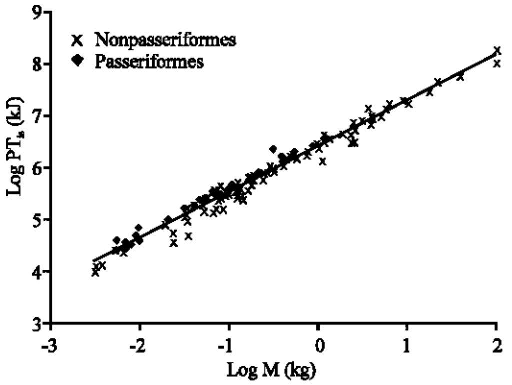

Fig. 1: The relationship between the total metabolic energy per maximum life span (PT_{1s}, kJ) and the body mass (M, kg) for 95 Nonpasserine and 32 Passerine birds

For life span in captivity, the allometric analysis have shown that a near to linear relationship between the total metabolic energy per life span and the body mass of birds in log-log plot holds too:

7 $PT_{1sc} = A^0_{1sc} M^{0.8776}$ ($R^2 = 0.9765$) with linear coefficient $A^0_{1sc} = 37.2\times10$ kJ kg^{-1}

Separately, for Passerine and Nonpasserine birds, the relationships between the total metabolic energy per life span and body mass (for maximum and life span in captivity) are given in Table 2.

For maximum and life span in captivity, the mean values of linear coefficient ($\bar{A}_{ls} \pm S_A$) for 24 studied orders, are given in Table 3.

The received results show that for all birds, the power coefficient in the 'lifespan metabolism-mass' relationship fall in the interval 0.8776-0.934. The width (0.057) of this interval is about the distance (0.066) from 0.934 to value 1.0, at which the 'lifespan metabolism-mass' relationship becomes exactly linear (isometric). Consequently, for birds

Table 2: The relationship between the total metabolic energy per life span PT_{ls} (kJ d^{-1}) and the body mass M (kg) for all birds and separately for Passerine and Nonpasserine

Aves	$PT_{ls} = A^0_{ls} M^k$	R^2	$PT_{lsc} = A^0_{lsc} M^k$	R^2
Passerine birds	$PT_{ls} = 36.728 \times 10^5 M^{0.9347}$	0.9872	$PT_{lsc} = 51.4 \times 10^5 M^{0.9077}$	0.9866
Nonpasserine birds	$PT_{ls} = 25.199 \times 10^5 M^{0.926}$	0.98	$PT_{lsc} = 35.13 \times 10^5 M^{0.8988}$	0.98
All birds	$PT_{ls} = 26.866 \times 10^5 M^{0.9037}$	0.9767	$PT_{lsc} = 37.2 \times 10^5 M^{0.8776}$	0.9765

Table 3: The mean values of the coefficients $\hat{A}_{ls}$, kJ kg^{-1} (for maximum life span) and $\hat{A}_{lsc}$, kJ kg^{-1} (for life span in captivity) for 24 orders. Legend: $\hat{A}_{ls} \pm S_A$ (mean±standard error)

No	Order of birds	$\bar{A}_{ls} \pm S_A \times$ 10 (kJ kg^{-1})	$\bar{A}_{lsc} \pm S_{ac} \times$ 10 (kJ kg^{-1})	N number of birds
1	Struthioniformes	15.21±4.37	18.91±5.4	2
2	Rheiformes	22.10	28.57	1
3	Casuariiformes	16.18±0.58	20.865±0.97	2
4	Apterygiformes	12.66±0.24	17.47±0.213	3
5	Sphenisciformes	27.11±2.78	37.046±3.928	6
6	Procellariiformes	31.9±3.6	43.63±4.558	5
7	Pelecaniformes	27.88±0.29	38.42±0.5728	4
8	Ciconiiformes	27.65±1.64	36.56±2.22	4
9	Anseriformes	30.34±2.256	42.846±3.65	6
10	Charadriiformes	32.60±2.01	46.82±3.518	5
11	Columbiformes	27.76±0.744	40.085±1.129	5
12	Falconiformes	23.7±2.36	32.914±3.84	5
13	Galliformes	29.7±2.94	42.13±4.62	4
14	Gruiformes	24.5±2.88	34.62±4.86	4
15	Psittaciformes	38.13±2.8	56.48±4.88	5
16	Cuculiformes	30.71±5.185	45.65±7.23	5
17	Strigiformes	22.2±0.81	32.39±1.39	5
18	Caprimulgiformes	19.95±2.93	29.77± 4.157	5
19	Apodiformes	35.9±2.1	56.25±2.93	6
20	Coliiformes	45.8±3.02	69.42±4.62	5
21	Trogoniformes	27.4	41.5	1
22	Coraciiformes	31.22±2.03	48.33±3.25	4
23	Piciformes	34.9±0.47	53.01±0.63	3
24	Passeriformes	45.08±1.85	68.42±3.05	32

the 'lifespan metabolism-mass' relationship is not exactly isometric, in comparison to Poikilotherms and Mammals. Reviews by Atanasov (2005a, 2007) show that 'lifespan metabolism-mass' relationships in Poikilotherms and Mammals scale approximately as 1.0 widely within and among taxa, in spite of variations in the metabolic and the lifetime exponents. In Poikilotherms (from Protozoa with mass 1×10^{15} kg^{-1} to Reptilia with mass 0.5×10 kg^{-1}) the power coefficient in relationships varied around 1.0 in interval 0.97-1.08. In Mammals (from mouse with mass 3×10^3 kg^{-1} to Elephant with mass 3×10^3 kg^{-1}) the power coefficient varied around 1.0 too, in interval 0.95-1.05. But, in Aves (Passeriformes and Nonpasseriformes) the variation of power coefficient in 'lifespan metabolism-mass' relationships is in interval 0.8776-0.934, possibly around middle value of this interval, equal to 0.906.

Nagy (1987, 2005) using ‘doubly labeled water technique’ showed that the field metabolic rate for all birds is proportional to $M^{0.681}$. If in 'lifespan metabolism-mass' relationship [6] and [7] we replace the data for basal metabolic rate with data for field metabolic rate, we shall received the power coefficients near to 0.9 too, like in relationships for basal metabolic rate. For example: for field metabolic rate (which is proportional to $M^{0.681}$), maximum life span (which is proportional to $M^{0.216}$) and life span in captivity (which is proportional to $M^{0.19}$) we shall received equations with power coefficients in the interval 0.871-0.897. This shows that for field metabolic rate the 'lifespan metabolism-mass' relationship is near to linear too, but not isometric.

It is very interesting the fact, that, respectively evolutionary range of animals (Poikilotherms, Mammals and Aves) the power coefficient fall from maximum 1.08 (in Poikilotherms) to 1.05 (in Mammals) to 0.934 (in Aves). Since the birds are the latest evolutionary branch, it is logically to suppose that the power coefficient in birds will be the lowest. In contrary, respectively evolutionary range of animals in 'lifespan metabolism-mass' relationships, the linear coefficients A_{ls} grow from $A^*_{ls} = 3.7 \times 10$ kJ kg^{-1} in Poikilotherms (Atanasov, 2005a), to $A^+_{ls} = 7.158 \times 10$ kJ kg^{-1} in Mammals (Atanasov, 2007) and to $A^0_{ls} = 26.86 \times 10$ kJ kg^{-1} in Aves. From evolutionary point of view the birds have the highest total metabolic energy, per life span, per unit body mass. The linear coefficient A_{ls} in the Aves has grown approximately 3.5 times in comparison to Mammals and 7.0 times in comparison to Poikilotherms. This show that A_{ls} grows not in arithmetical, but in geometrical progression, which means acceleration of the evolutionary processes in the course of time. However, Zotin and Lamprecht (1996) come to the idea of acceleration of the evolutionary processes too, analyzing the linear coefficients a in 'metabolism-mass' relationships $P = aM^k$ for Poikilotherms, Mammals and Aves.

Table 3 shows that the values of $\bar{A}_{ls}$ differ across bird’s orders. The difference is about 3.5 times from big birds from Nonpasseriformes orders (Struthioniformes, Rheiformes, Casuariiformes, Apterygiformes) to small birds from Nonpasseriformes (Apodiformes, Coliiformes, Psittaciformes, Piciformes) and small Passeriformes birds. For example, the coefficient $\bar{A}_{ls}$ grows from about $(12 \div 17) \times 10$ kJ kg^{-1} in Struthioniformes, Rheiformes, Casuariiformes and Apterygiformes to about $(35 \div 45) \times 10$ kJ kg^{-1} in Apodiformes, Coliiformes, Psittaciformes, Piciformes and Passeriformes. The coefficient $\bar{A}_{ls}$ grows maximum in Coliiformes and Passerifomes, up to 45×10 kJ kg^{-1} . The higher value of $\bar{A}_{ls}$ in Passerine birds can be connected with the relatively small body mass of these birds (from 0.0055-1.2 kg) and the relatively higher basal metabolic rate, per unit body mass and not because of their belonging to order Passerine. For example, $\bar{A}_{ls}$ for

Nonpasseriformes orders Coliiformes, Psittaciformes, Apodifomes and Piciformes is about $(35 \div 45.8)\times 10$ kJ kg^{-1} versus 45.08×10 kJ kg^{-1} in Passeriformes order. In addition, $\bar{A}_{ls}$ in Nonpasseriformes order (Coliiformes) is higher than $\bar{A}_{ls}$ in Passeriformes. Consequently, our survey shows that the changes of the body mass, basal metabolic rate and life span of birds are 3 mutually related parameters, so that the product $A_{ls} = (P\ T_{ls})\ /M$ remains relatively constant, in comparison to 5 orders of magnitude variation of the body mass and the total metabolic energy per life span. For example, across the 127 individuals A_{ls} changes less than 10 fold. The difference in the values of A_{ls} depends on other biological, physiological, ecological factors, physical activity, cold exposure, diet, reproduction, body composition, daily rhythm and others (Sparti *et al*., 1977; Speakman and Selman, 2003; Nagy, 2005; White and Seymour, 2005). The influence of these factors on metabolic rate and life span in birds is very high, in comparison to Poikilotherms and Mammals and this leads to have not isometric relationship between the lifespan energy and the body mass. However, the further study of A_{ls} for bird's orders and species could uncover a new knowledge for the energetic of living organisms.

Possibly, the linearity between the total metabolic energy per life span and body mass expresses a general allometric law in animal energetics (Atanasov, 2005b), since it is valid for Poikilothetms, Mammals and approximately for Aves too.

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