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THE NEAR TO LINEAR ALLOMETRIC RELATIONSHIP BETWEEN TOTAL METABOLIC ENERGY PER LIFE SPAN AND BODY MASS OF NONPASSERINE BIRDS

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Summary

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The bioenergetic studies on animals have shown that the basal rate of metabolism P(kJ/d) is related to the body mass M (kg) of the 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 connection between the total metabolic energy per life span PTls (kJ) and the body mass M (kg) of nonpasserine birds (with Tls – life span in days). Using statistical analyses it was shown that a near to linear relationship existed between the total metabolic energy per life span and the body mass of nonpasserine birds (class Aves), belonging to 23 orders (Struthioniformes, Rheiformes, Casuariiformes, Apterygiformes, Sphenisciformes, Procellariiformes, Pelecaniformes, Ciconiiformes, Anseriformes, Charadriiformes, Columbiformes, Falconiformes, Galliformes, Gruiformes, Psittaciformes, Cuculiformes, Strigiformes, Caprimulgiformes, Apodiformes, Coliiformes, Trogoniformes, Coraciiformes and Piciformes) of the type: $PT_{ls}= A^0_{ls} \times M^{0.939}$ with correlation coefficient of $R^2=0.97$. The linear coefficient $A^0_{ls} = 29.4\times10^5$ kJ/kg is the total metabolic energy, exhausted during the life span per 1 kg body mass of birds. This linear coefficient can be regarded as a relatively constant metabolic parameter for nonpasserine birds, in spite of 10^5 fold differences between the body mass of birds. The mean values of linear coefficient $\bar{A}_{ls}$ for the 23 studied orders differed 4.65 times between big birds (order Struthioniformes) and small birds (order Psittaciformes), since $\bar{A}_{ls}$ grew from 12.5×10^5 kJ/kg in order Struthioniformes to 58.13×10^5 kJ/kg in order Psittaciformes. The mean $\bar{A}_{ls}$ values for 23 orders were nearly multiple to 3×10^5kJ/kg. The energy of 3×10^5kJ/kg was exhausted from 1 kg body mass of big and small birds for the periods when the sexual maturity was reached.

Key words: basal rate of metabolism, life span, nonpasserine birds, total metabolic energy

INTRODUCTION

The patterns existing between body size or mass and the other fundamental features of living organisms are generally described by a power function called an 'allometric' one.

The bioenergetic studies on poikilothermic animals, mammals and birds (Hemmingsen, 1960; Kleiber, 1961; Schmidt-Nielsen, 1984; Heusner, 1985; McNab, 1988; Chen & Li, 2003; Agutter & Wheatley, 2004; Speakman, 2005) have shown that the basal rate of metabolism P(kJ/d) is related to the body mass M(kg) as expressed by an equation of type $P=aM^k$. The biological meaning of the linear coefficient *a* and the power coefficient *k* can be connected with the bioenergetic evolution (Zotin & Lamprecht, 1996; Atanasov & Dimitrov, 2002).

In previous works, Atanasov (2005a, b; 2007) inserted the life span (T_{ls}) of animals as a parameter, showing that the relationships between the total metabolic energy per life span ($P_{ls} = PT_{ls}$) and body mass (M) over a broad number of animals (class poikilotherms, mammals and birds) was nearly expressed by the linear equation of type $P_{ls}=A_{ls}M$. The linear coefficient A_{ls} has the meaning of total metabolic energy exhausted from 1 kg body mass of an animal during its life span. As a result, the total metabolic energy P_{ls} that is exhausted from an animal is the product of A_{ls} and its body mass M.

The mean values of this total metabolic energy per life span, per 1 kg body mass ($\bar{A}_{ls}$) for multicellular poikilotherms increase from 0.5×10^5 kJ/kg in snakes to maximum value of $(5\div6)\times10^5$ kJ/kg in other reptiles. The values of $\bar{A}_{ls}$ for others poikilothermic fall between these two values (Atanasov, 2005a).

The mean values of total metabolic energy per life span, per 1 kg body mass for mammals increase from 4.66×10^5 kJ/kg in order Didelphi (American marsupials) to about 18.1×10^5 kJ/kg in order Primata (primates) (Atanasov, 2005b; 2007).

A prognostic estimation of this energy for the nonpasserne birds (class Aves) can be made from the relation of Lasiewski & Dawson (1967) about the rate of metabolism: $P=78.3\times M^{0.723}$ (P in kcal/d; M in kg) and the formula of Lindstedt & Calder (1976; 1981) for longevity of birds (in cage): $T_{ls}=28.3\times M^{0.19}$ (T_{ls}, years; M, kg). Using the relation $A_{ls} = (PT_{ls})/M$ we can calculate the total metabolic energy per life span, utilized per 1 kg body mass as a function of body mass:

$$A_{ls} = (33.32\times10^5)\times M^{-0.087}, \text{ kJ/kg}$$

This formula shows that A_{ls} depends slightly on body mass of birds ($\sim M^{-0.087}$). Indeed, for birds with a 10^5-fold difference in body masses, the computation values of A_{ls} changes 2.5-fold: from 22.3×10^5 kJ/kg (for *Struthio camelus* with body mass ~100 kg) to 55.25×10^5 kJ/kg (for apodiform birds with body mass ~3 g). Therefore, the values of A_{ls} for birds are higher than values of A_{ls} for poikilotherms and mammals, but have nearly the same order of magnitude ($\sim10^5$ kJ/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 nonpasserine birds with variation in the body mass of about 5 orders of magnitude.

DATA AND METHODS

Estimates of basal rate of metabolism (P), body mass (M) and life span (T_{ls}) are assembled in Table 1 for 95 individual species, including 23 orders of nonpasserine birds (class Aves): 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 basal rate of metabolism and body mass of birds are obtained from Bennett & Harvey (1987). The life span of birds was calculated from formula of Lindstedt & Calder (1976):

$T_{ls}=28.3\times M^{0.19}$ (T_{ls} in years; M in kg)

Table 1. Data for the body mass (M), basal rate of metabolism (P) , life span (T_{ls}), 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) (A_{ls}) for 95 nonpasseriform birds from 23 orders

Avian orders	M (kg) *	P (kJ/d) *	T_{ls}(y)**	PT_{ls} (kJ)	A_{ls} (kJ/kg)
Order Struthioniformes					
1. *Struthio camelus*	100	9823	45	161.3×10^6	16.1×10^5
2. *Struthio camelus*	100	5442.3	45	89.4×10^6	8.9×10^5
Order Rheiformes					
3. *Rhea americana*	21.7	3344	50	61×10^6	28×10^5
Orger Casuariiformes					
4. *Casuarius bennetti*	17.6	2156.9	50	39.36×10^6	22.36×10^5
5. *Dromaius novaehollandiae*	38.925	3746.1	45	61.5×10^6	15.8×10^5
Order Apterygiformes					
6. *Apteryx australis*	2.38	347.77	28	35.5×10^5	14.9×10^5
7. *Apteryx owenii*	1.095	178.486	24	15.65×10^5	14.3×10^5
8. *Aptreryx haastii*	2.54	360.734	28	36.86×10^5	14.5×10^5
Order Sphenisciformes					
9. *Pygoscelis papua*	6.29	1603.45	35	20.48×10^6	32.56×10^5
10. *Pygoscelis adeliae*	3.97	1055.87	32	12.3×10^6	30.98×10^5
11. *Eudyptes pachyrhynchus*	2.6	597.32	28	61×10^5	23.5×10^5
12. *Eudyptes chrysocome*	2.506	862	28	88×10^5	35.1×10^5
13. *Eudyptes chrysocome*	2.33	503.7	28	51.5×10^5	22.1×10^5
14. *Eudyptula albosignata*	1.15	570.57	24	50×0^5	43.5×10^5
Order Procellariiformes					
15. *Macronectes giganteus*	3.63	1492.68	30	16.3×10^6	44.9×10^5
16. *Pterodroma hypoleuca*	0.18	89.87	15	4.92×10^5	27.3×10^5
17. *Pterodroma mollis*	0.274	150.9	18	9.9×10^5	36.1×10^5
18. *Pachyptila salvini*	0.165	133.76	15	7.32×10^5	44.36×10^5
19. *Puffinus griseus*	0.740	249.13	18	16.36×10^5	22.1×10^5
Order Pelecaniformes					
20. *Pelecanus occidentalis*	3.038	894.5	35	11.4×10^6	37.6×10^5
21. *Sula dactylatra*	1.289	475.26	29	50.3×10^5	39×10^5
22. *Sula sula*	1.017	375.78	28	38.4×10^5	37.76×10^5

Table 1. (cont'd)

Avian orders	M (kg) *	P (kJ/d) *	T_{ls}(y)**	PT_{ls} (kJ)	A_{ls} (kJ/kg)
23. *Phalacrocorax auritus*	1.33	474	29	50.2×10^5	37.7×10^5
Order Ciconiiformes					
24. *Ardea herodias*	1.87	535	31	60.54×10^5	32.4×10^5
25. *Egretta tricolor*	0.31	147.55	18	9.5×10^5	30.6×10^5
26. *Mycteria americana*	2.5	840.18	33	101.2×10^5	40.5×10^5
27. *Leptoptilos javanicus*	5.71	1283.2	39	182.66×10^5	32×10^5
Order Anseriformes					
28. *Cygnus buccinator*	8.88	1747.24	40	255×10^5	28.7×10^5
29. *Branta bernicla*	1.168	390.4	29	41.3×10^5	35.36×10^5
30. *Aix sponsa*	0.485	271.7	24	23.8×10^5	49×10^5
31. *Anas platyrhynchos*	1.132	434.7	25	39.6×10^5	35×10^5
32. *Anas crecca*	0.25	143.8	20	10.5×10^5	42×10^5
33. *Anas querquedula*	0.289	192.7	20	14×10^5	48.44×10^5
34. *Aythya fuligula*	0.574	233.2	20	17×10^5	29.6×10^5
Order Charadriiformes					
35. *Tringa ochropus*	0.09	79.4	10	2.9×10^5	32.2×10^5
36. *Stercorarius skua*	0.97	409.6	25	37.4×10^5	38.56×10^5
37. *Larus delawarensis*	0.439	249.13	20	18.2×10^5	41.45×10^5
38. *Larus occidentalis*	0.761	293	20	21.3×10^5	28×10^5
39. *Gygis alba*	0.0981	70.22	15	3.84×10^5	39.1×10^5
Order Columbiformes					
40. *Columba* unicincta	0.318	148	20	10.8×10^5	34×10^5
41. *Columba livia*	0.315	150	20	10.95×10^5	34.76×10^5
42. *Columba* livia	0.266	140.87	20	10.3×10^5	38.7×10^5
43. Streptopelia *decaocto*	0.187	110	20	8.03×10^5	43×10^5
Order Falconiformes					
44. *Vultur gryphus*	10.32	1467.18	40	21.4×10^6	20.7×10^5
45. *Falco sparverius*	0.117	72.73	15	4×10^5	34.2×10^5
46. *Accipiter nisus*	0.135	81.93	19	5.68×10^5	42×10^5
47. *Buteo buteo*	1.012	324.37	28	33.15×10^5	32.75×10^5
48. *Gypaetus barbatus*	5.07	953	30	104.3×10^5	20.75×10^5
Order Galliformes					
49. *Lagopus lagopus*	0.524	268.36	18	18.81×10^5	35.9×10^5
50. Lagopus *lagopus*	0.509	294.7	18	19.36×10^5	38×10^5
51. *Callipepla gambelii*	0.126	65.21	10	2.38×10^5	18.88×10^5
52. *Gallus* gallus	2.43	670.47	16	39.155×10^5	16×10^5

Table 1. (cont'd)

Avian orders	M (kg) *	P (kJ/d) *	T_{ls}(y) **	PT_{ls} (kJ)	A_{ls} (kJ/kg)
Order Gruiformes					
53. *Grus canadensis*	3.89	702.2	25	64×10^5	16.45×10^5
54. *Anthropoides paradiseus*	4.03	919.6	25	83.9×10^5	20.8×10^5
55. *Crex crex*	0.096	68.13	15	3.73×10^5	38.85×10^5
56. *Fulica atra*	0.412	176	20	12.85×10^5	31.2×10^5
Order Psittaciformes					
57. *Melopsittacus undulatus*	0.0337	41.38	15	2.265×10^5	67.2×10^5
58. *Myiopsitta monachus*	0.0815	67.72	18	4.45×10^5	54.6×10^5
59. *Myiopsitta monachus*	0.0831	68.13	18	4.47×10^5	53.8×10^5
60. *Myiopsitta monachus*	0.0831	59	18	3.87×10^5	46.57×10^5
61. *Neophema pulchella*	0.04	50.16	15	2.74×10^5	68.5×10^5
Order Cuculiformes					
62. *Cuculus canorus*	0.128	108.26	17	6.7×10^5	52.3×10^5
63. *Eudynamys scolopacea*	0.188	142.12	17	8.8×10^5	46.8×10^5
64. *Cacomantis variolosus*	0.0238	16.3	12	0.71×10^5	29.8×10^5
65. *Cacomantis variolosus*	0.0238	10.45	12	0.46×10^5	19.3×10^5
66. *Centropus senegalensis*	0.175	130	17	8.06×10^5	46×10^5
Order Strigiformes					
67. *Athene cunicularia*	0.1427	58.52	19	4.06×10^5	28.45×10^5
68. *Glaucidium cuculoides*	0.163	74.82	20	5.46×10^5	33.5×10^5
69. *Strix aluco*	0.52	179.74	25	16.4×10^5	31.54×10^5
70. *Aegolius acadicus*	0.124	56.43	19	3.91×10^5	31.53×10^5
71. *Asio otus*	0.240	110.35	22	8.86×10^5	37×10^5
Order Caprimulgiformes					
72. *Podargus ocellatus*	0.145	48.9	15	2.68×10^5	18.5×10^5
73. *Chordeiles minor*	0.072	38	12	1.66×10^5	23×10^5
74. *Caprimulgus europaeus*	0.0774	55.59	12	2.43×10^5	31.4×10^5
75. *Phalaenoptilus nuttallii*	0.035	13.376	12	0.586×10^5	16.74×10^5
76. *Eurostopodus mystacalis*	0.088	35.11	13	1.67×10^5	18.9×10^5

Table 1. (cont'd)

Avian orders	M (kg) *	P (kJ/d) *	T_{ls}(y) **	PT_{ls} (kJ)	A_{ls} (kJ/kg)
Order Apodiformes					
77. *Calypte anna*	0.0054	9.9	4	14.45×10^3	26.76×10^5
78. *Calypte costae*	0.0032	4.476	4	6.5×10^3	20.3×10^5
79. *Eugenes fulgens*	0.0066	8.6	4	12.55×10^3	19×10^5
80. *Selasphorus platycercus*	0.003	5.79	4	8.45×10^3	28.16×10^5
81. *Patagona gigas*	0.0191	24.74	8	72.24×10^3	37.8×10^5
82. *Archilochus alexandri*	0.0033	6.27	4	9.15×10^3	27.7×10^5
Order Coliiformes					
83. *Colius striatus*	0.0512	46.8	12	2×10^5	39×10^5
84. *Colius castanotus*	0.069	89.45	12	3.9×10^5	56.5×10^5
85. *Colius castanotus*	0.0577	66	12	2.9×10^5	50.26×10^5
86. *Urocolius macrourus*	0.0485	63.5	12	2.8×10^5	57.7×10^5
87. *Urocolius indicus*	0.0535	61.86	12	2.7×10^5	50.46×10^5
Order Trogoniformes					
88. *Trogon rufus*	0.053	37.2	12	1.6×10^5	30.2×10^5
Order Coraciiformes					
89. *Alcedo atthis*	0.0343	32.6	10	1.19×10^5	34.7×10^5
90. *Upupa epops*	0.067	47.65	12	2.08×10^5	31×10^5
91. *Merops viridis*	0.0338	25.5	10	0.93×10^5	27.5×10^5
92. *Merops viridis*	0.0338	33.86	10	1.2×10^5	35.5×10^5
Order Piciformes					
93. *Jynx torquilla*	0.0318	30.9	10	1.12×10^5	35.2×10^5
94. *Dendrocopus major*	0.098	77.3	15	4.23×10^5	43.2×10^5
95. *Dendrocopus major*	0.117	89.87	15	4.92×10^5	42.05×10^5

*The data for M and P are obtained from Bennett & Harvey (1987); ** The life span was calculated from formula of Lindstedt & Calder (1976) and corrected according to data from literature sources (Sokolov, 1990; Naumov & Kuzjakina, 1971).

and corrected accordingly for the longevity data given in literature sources (Sokolov, 1990, Naumov & Kuzjakina, 1971).

For each bird, the total metabolic energy per life span PT_{ls} (kJ) was calculated as a product from the rate of metabolism P(kJ/d) and life span T_{ls}(d). The total metabolic energy per life span, per 1 kg body mass A_{ls} (kJ/kg) was calculated as a ratio of PT_{ls} (kJ) and body mass M(kg): $A_{ls}=(PT_{ls})/M$. The statistical software "STATISTICA" from the Space Research Institute (BAS) Bulgaria was used for all calculations.

RESULTS

The data about studied avian species, the body mass, the basal rate of metabolism, the life span, 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 the body mass (M) of Aves is presented on Fig. 1.

Statistical analysis showed that a near to linear relationship between the total metabolic energy per life span and the body mass of birds holds:

$$\log (PT_{ls})=6.4685 +0.939 \log M \qquad (1)$$

with R^2=0.97

If $\log A^0_{ls}$=6.4685, the above equation can be presented as:

$$\log(PT_{ls}) = \log(A^0_{ls} M^{0.939}) \qquad (2)$$

and further:

$$PT_{ls} = A^0_{ls} M^{0.939} \qquad (3)$$

with linear coefficient A^0_{ls}=29.4×10^5 kJ/kg.

The correlation coefficient between PT_{ls} and M is equal to R^2=0.97. This means that A^0_{ls} = PT_{ls}/M= 29.4x10^5 kJ/kg in the 23 studied orders is a relatively constant parameter for all nonpasserine birds.

The individual values of A_{ls} for all 95 studied species of birds are given in Table 1. The logarithmic graphic of the relationship between the total metabolic energy per life span and the body mass only for 19 orders (without big birds from orders Struthioniformes, Rheiformes, Casuariiformes and small birds from order Apodiformes) is from the type $PT_{ls}=A^0_{ls} \times M^{0.926}$ with R^2=0.977 and linear coefficient A^0_{ls}=30.49x10^5 kJ/kg.

The mean values of alometric coefficient $\bar{A}_{ls} \pm S_A$ for different orders in Table 1 are given in Table 2.

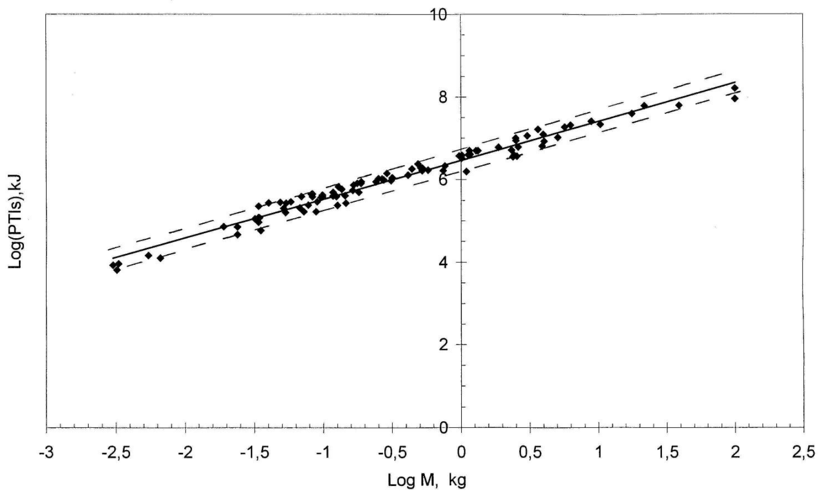

Fig. 1. Relationship between the total metabolic energy per life span (PT_{ls}, kJ) and the body mass (M, kg) of 95 nonpasserine bird species from 23 orders. The 95% confidence limits are shown by dashed lines.

Table 2. The mean values of total metabolic energy per life span, per 1 kg body mass ($\bar{A}_{ls}$, kJ/kg) for 23 orders of birds

Orders	Number of avian species	$\bar{A}_{ls} \pm S_A$, kJ/kg
1. Struthioniformes	2	$(12.5 \pm 3.6) \times 10^5$
2. Rheiformes	1	28×10^5
3. Casuariiformes	2	$(19.08 \pm 3.28) \times 10^5$
4.Apterygiformes	3	$(14.57 \pm 0.176) \times 10^5$
5.Sphenisciformes	5	$(31.3 \pm 3.2) \times 10^5$
6.Procellariiformes	5	$(34.95 \pm 4.54) \times 10^5$
7.Pelecaniformes	4	$(38 \pm 0.33) \times 10^5$
8.Ciconiiformes	4	$(33.875 \pm 2.24) \times 10^5$
9.Anseriformes	6	$(39.75 \pm 3.3) \times 10^5$
10.Charadriiformes	5	$(35.86 \pm 2.5) \times 10^5$
11.Columbiformes	5	$(36 \pm 2.23) \times 10^5$
12.Falconiformes	5	$(30 \pm 4.13) \times 10^5$
13.Galliformes	4	$(27.2 \pm 4.4) \times 10^5$
14.Gruiformes	4	$(26.8 \pm 5.06) \times 10^5$
15.Psittaciformes	5	$(58.13 \pm 4.2) \times 10^5$
16.Cuculiformes	6	$(38.8 \pm 6.16) \times 10^5$
17.Strigiformes	5	$(32.4 \pm 1.4) \times 10^5$
18.Caprimulgiformes	5	$(21.7 \pm 2.64) \times 10^5$
19.Apodiformes	6	$(26.62 \pm 2.75) \times 10^5$
20.Coliiformes	5	$(50.78 \pm 3.3) \times 10^5$
21.Trogoniformes	1	30.2×10^5
22.Coraciiformes	4	$(32.2 \pm 1.84) \times 10^5$
23.Piciformes	3	$(40.15 \pm 2.5) \times 10^5$

DISCUSSION

Our survey shows that the changes of body mass, basal rate of metabolism and life span of nonpasserine birds are three mutually related parameters, so that the relation $A_{ls} = (PT_{ls})/M$ remains relatively constant. The mean values of $\bar{A}_{ls}$ for 23 orders differ 4.65-fold from 12.5×10^5 kJ/kg in order Struthioniformes to 58.13×10^5 kJ/kg in order Psittaciformes, in spite of $\sim10^5$ fold differences between the body mass and total metabolic energy per life span of birds.

For example, the body mass of studied nonpasserine birds varied from minimum value $(3.0\div19.1)\times10^{-3}$ kg in order Apodiformes to maximum value 100 kg in order

Struthioniformes. The total metabolic energy per life span (P_{ls}) varied from $(6.5 \div 72.24) \times 10^3$ kJ in order Apodiformes to $(0.89 \div 1.6) \times 10^8$ kJ in order Struthioniformes.

The mean values of the coefficient $\bar{A}_{ls}$ for other orders gives us a base to classify avian orders in ascending order according $\bar{A}_{ls}$ (Fig. 2). A similar classification for poikilothermic animals, mammals and birds is made from Zotin & Lamprecht (1996), but on the basis of increasing linear coefficients *a* in the power relation $P = aM^k$.

Since the coefficient $\bar{A}_{ls}$ has a dimension of physical and chemical potential (J/kg) it could has the meaning of bioenergetic metabolic potential. Relatively small birds from orders Piciformes, Coliiformes and Psittaciformes have near to the maximum bioenergetic metabolic potential as is observed in Fig. 2. Near to the minimum bioenergetic metabolic potential is characteristic for big birds of orders Struthioniformes, Apterygifomes, Casuariiformes and Caprimulgiformes.

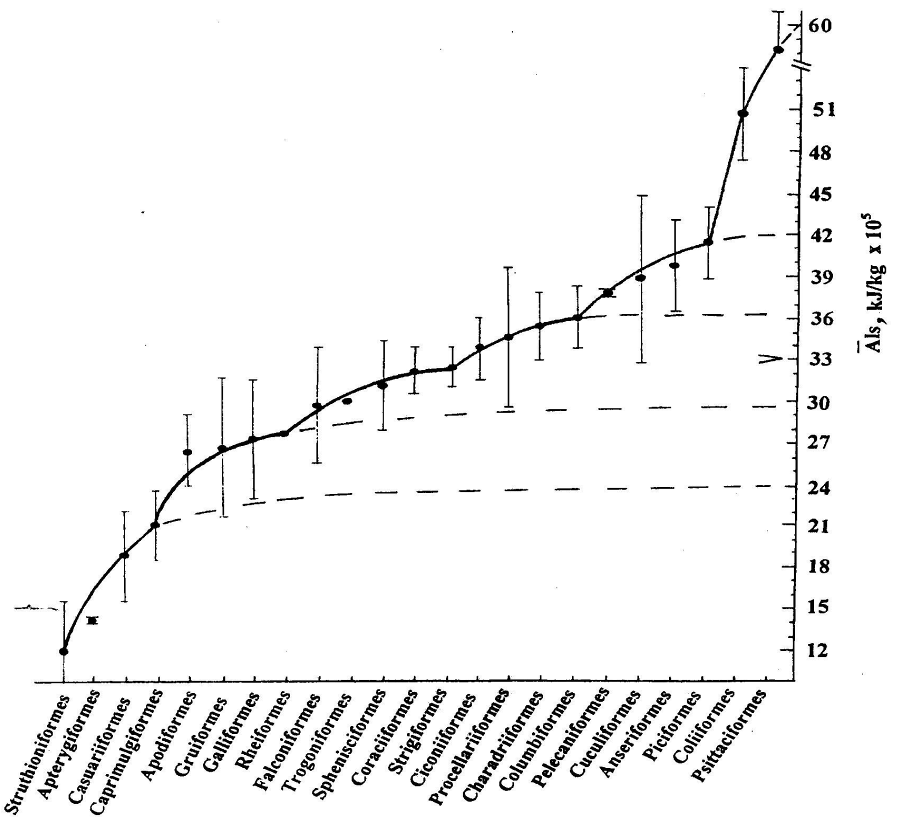

Fig. 2. Mean values of total metabolic energy per life span, per 1kg body mass ($\bar{A}_{ls}$, kJ/kg) for 23 orders of birds. X-axis: birds orders; Y-axis: $\bar{A}_{ls} \pm$ SEM.

It is very interesting, that mean $\bar{A}_{ls}$ values for 23 orders are nearly multiples to 3×10^5 kJ/kg. For example, $\bar{A}_{ls}$ can be expressed as $\bar{A}_{ls}$ =(n±0.1) 3×10^5 kJ/kg , or $\bar{A}_{ls}$ =(n±0.2) 3×10^5 kJ/kg, or $\bar{A}_{ls}$ =(n±0.33) 3×10^5 kJ/kg, where *n* is an integer positive number, varying from 4 (in order Struthioniformes) to 19 (in order Psittaciformes).

Fig. 2 shows that the values of $\bar{A}_{ls}$ form the zone of values, asymptotically close to maximum values 24, 30, 33, 36, 42 and 60 ($\times10^5$ kJ/kg), that are multiple to 3×10^5 kJ/kg too.

Using the relation $PT_{ls} = A^0_{ls}M$, we receive the inverselyproportional relation between the life span (T_{ls}, d) and the metabolic rate per unit body mass i.e. the intensity of metabolism P*, kJ/(d×kg):

$T_{ls} = A_{ls} / P^*$, where $P^* = P/M$.

We can calculate the time for exhausting 3×10^5kJ/kg from 1kg body mass of the birds using a modification of this formula:

$T = 3\mathrm{x}10^5 / P^*$, (in days).

The calculation shows that the time T is very close to the time period for sexual maturity of birds: about 1–2 years for small birds and 3–6 years for big birds (Naumov & Kuzjakina, 1971). For example, in order Pelecaniformes with mean body mass of birds M=1.67 kg, mean rate of metabolism P=555 kJ/d and mean intensity of metabolism P*=P/M=332 kJ/(d×kg), we received a time period of 2.47 years for exhausting 3×10^5 kJ energy. The same energy (3×10^5 kJ) for a big Andean condor (*Vultur gryphus)* with body mass 10.3 kg, rate of metabolism P=1467.18 kJ/d and intensity of metabolism P*= 142 kJ/(d×kg) would be exhausted for 5.78 years. For a small common teal (*Anas crecca)* with body mass 0.25 kg, rate of metabolism 143.8 kJ/d and intensity of metabolism P*=575.2 kJ/(d×kg), this energy would be exhausted for T=1.7 years. For very small birds Apodiformes: Trochilidae with mean body mass of order 0.0068 kg, mean rate of metabolism ~10 kJ/d and mean intensity of metabolism 1470 kJ/(d×kg), this energy would be exhausted for T=204 days. However, an additional statistical approach is necessary to find a consistent relationship between the total metabolic energy (3×10^5 kJ) exhausted from 1 kg body mass and the time for sexual maturity of birds.The further study of A_{ls} for a bigger number of birds orders and species could help to gain new knowledge about bioenergetics of living organisms.

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