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BRAIN SIZE IN BIRDS: 4. PASSERIFORMES

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Abstract. Brain size in 151 species and its relation to body size in 10 families of birds are estimated. The order Passeriformes is considered.

INTRODUCTION

This is the final part of my review of the brain size in birds (Mlíkovský, 1989 a, b, c). See Mlíkovský (1989a) for the sections on Material and Methods.

RESULTS AND DISCUSSION

Passeriformes

The data on the brain size and the body size in Passeriformes are presented in the Table 1 and Figures 1—7. The data were sufficient for the discussion of the brain — body size relationships in 12 families only (see below). No data were available for the following families: Dendrocolaptidae, Rhinocryptidae, Pipridae, Oxyruncidae, Atrichornithidae, Xenicidae, Pittidae, Philepittidae, Campephagidae, Irenidae, Vangidae, Dulidae, Climacteridae, Rhabornithidae, Remizidae, Dicaeidae, Zosteropidae, Meliphagidae, Dicruridae, Callaeidae, Grallinidae, Artamidae. Ptilonorhynchidae, Paradisaeidae and Drepanididae.

In Motacillidae, brain size and body size are only marginally correlated ($r_s = 0.725$; $p < 0.1$). This is obviously an artifact, caused probably by the very restricted range of body size of the included species (17.5—21 g). See Smith (1980) for a statistical explanation. However, calculation of the regression equation is meaningless until this bias is removed.

In Turdidae, brain size and body size are positively correlated ($r_H = 1.875 \pm 0.277$; $p < 0.001$) and their allometrical relation is $E = 0.0809\ S^{0.712 \pm 0.0556}$ ($n = 14$). The slope of this regression is significantly higher than the Dubois' constant ($t_s = 2.734$; $p < 0.01$), but does not significantly differ from the Jerison's constant ($t_s = 0.815$; $p > 0.05$).

In Sylviidae, brain size and body size are positively correlated ($r_s = 0.935$; $p < 0.01$) and their allometrical relation is $E = 0.0803\ S^{0.712 \pm 0.107}$ ($n = 8$). The slope of this regression does not significantly differ from either the Dubois' constant ($t_s = 1.421$; $p > 0.05$) or the Jerison's constant ($t_s = 0.424$; $p > 0.05$).

In Paridae, brain size and body size are positively correlated ($r_S = 0.943$; $p < 0.01$) and their allometrical relation is $E = 0.188\ S^{0.549 \pm 0.101}$ ($n = 6$). The slope of this regression does not significantly differ from either the Dubois' constant ($t_s = -0.109$; $p > 0.05$) or the Jerison's constant ($t_s = -1.165$; $p > 0.05$).

In Nectariniidae, brain size and body size are positively correlated (r_S = = 1.000; $p < 0.05$) and their allometrical relation is $E = 0.156\ S^{0.486 \pm 0.136}$ (n = 4). The slope of this regression does not significantly differ from either the Dubois' constant ($t_s = -0.544$; $p > 0.05$) or the Jerison's constant (t_s = = −1.328; $p > 0.05$).

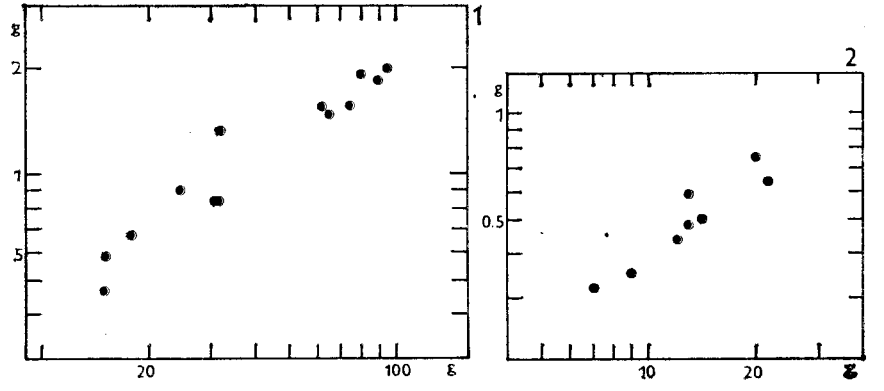


Fig. 1. Relationship between the brain size (Y axis) and the body size (X axis) in Turdidae. See Table 1 for exact data.
Fig. 2. Relationship between the brain size (Y axis) and the body size (X axis) in Sylviidae. See Table 1 for exact data.

In Corvidae, brain size and body size are positively correlated ($r_H = 1.949 \pm$ $\pm$ 0.302; $p < 0.001$) and their allometrical relation is $E = 0.162\ S^{0.648 \pm 0.0495}$ (n = = 12). The slope of this regression does not significantly differ from either the Dubois' constant ($t_s = 1.778$; $p > 0.05$) or the Jerison's constant (t_s = = −0.377; $p > 0.05$).

In Ploceidae, brain size and body size are positively correlated ($r_S = 1.000$; $p < 0.05$) and their allometrical relation is $E = 0.0706\ S^{0.737 \pm 0.218}$ (n = 4). The slope of this regression does not significantly differ from either the Dubois' constant ($t_s = 0.812$; $p > 0.05$) or the Jerison's constant ($t_s = 0.323$; $p > 0.05$).

In Estrildidae, brain size and body size are positively correlated (r_H = = 1.410 + 0.289; $p < 0.001$) and their allometrical relation is $E = 0.0984\ S^{0.666 \pm 0.0843}$ (n = 13). The slope of this regression does not significantly differ from either the Dubois' constant ($t_s = 1.257$; $p > 0.05$) or the Jerison's constant (t_s = −0.008; $p > 0.05$).

In Fringillidae, brain size and body size are positively correlated (r_H = = 2.154 + 0.267; $p < 0.001$) and their allometrical relation is $E = 0.0857\ S^{0.756 \pm 0.0423}$ (n = 15). The slope of this regression is significantly higher than both the Dubois' constant ($t_s = 4.634$; $p < 0.001$) and the Jerison's constant ($t_s = 2.112$; $p < 0.05$).

In Parulidae, brain size and body size are positively correlated ($r_s = 0.808$; $p < 0.01$) and their allometrical relation is $E = 0.0622\ S^{0.799 \pm 0.114}$ (n = 9). The slope of this regression is significantly higher than the Dubois' constant ($t_s = 2.096$; $p < 0.05$), but does not significantly deviate from the Jerison's constant ($t_s = 1.161$; $p > 0.05$).

Table 1. Brain size and encephalization in Passeriformes

n = number of measured brains or cava cranii, S = body mass (g), E = brain mass (g), I_{rel} = relative brain mass (%), Q_r = coefficient of relative encephalization. See Mlíkovský (1989a) for the calculation of these indices. Author = who measured brains or cava cranii.

Taxon	n	S	E	I_{rel}	Q_r	Author
Eurylaimidae						
Cymbirhynchus macrorhynchus	2		1.5			22
Formicariidae						
Chamaeza campanisona	1		1.9			22
Cotingidae						
Pyroderus scutatus	2		4.45			22
Tyrannidae						
Colonia colonus	1		1.3			22
Phytotomidae						
Phytotoma rara	1		1.2			22
Menuridae						
Menura novaehollandiae	1	910	10.5	1.15		22
Alaudidae						
Alauda arvensis	18	35	0.98	2.80		2, 4, 12, 14
Melanocorypha calandra	4	55	1.36	2.47		12
Hirundinidae						
Hirundo rustica	15	18	0.55	3.06		12, 17
Hirundo senegalensis	3	20	0.53	2.65		6
Delichon urbica	5	15	0.44	2.93		12
Pycnonotidae						
Pycnonotus barbatus	3	41	1.17	2.85		6
Laniidae						
Lanius collurio	3	28	1.02	3.64		12, 14
Lanius collaris	3	31	1.11	3.58		6
Telophorus "senegalus"	2	52	1.40	2.69		6
Bombycillidae						
Bombycilla garrulus	7	50	1.82	3.64		12, 14, 19
Motacillidae						
Motacilla alba	6	21	0.64	3.05		12, 17
Motacilla flava	4	17.5	0.52	2.97		17
Anthus campestris	5	18	0.48	2.67		17

Taxon	n	S	E	I_{rel}	Q_r	Author
Anthus pratensis	3	19	0.53	2.79		12
Anthus trivialis	3	21	0.60	2.86		17
Cinclidae						
Cinclus cinclus	4	60	1.45	2.42		12
Troglodytidae						
Troglodytes troglodytes	12	9.5	0.49	5.16		1, 5, 10, 12
Mimidae						
Mimus polyglottos	5	45	1.46	3.24		2
Dumetella carolinensis	13	30	1.02	3.40		20
Prunellidae						
Prunella modularis	1	18	0.73	4.06		12
Muscicapidae						
Muscicapa striata	3	14	0.48	3.43		12, 14
Turdidae						
Turdus merula	41	90	1.84	2.04	– 7.65	2, 4, 9–13, 19
Turdus philomelos	10	65	1.49	2.29	– 5.71	12, 14
Turdus iliacus	8	75	1.53	2.04	– 12.56	13, 14
Turdus pilaris	5	95	2.00	2.11	– 3.41	14
Turdus migratorius	2	80	1.95	2.44	6.44	2, 8
Turdus pelios	3	62	1.55	2.50	1.44	6
Hylocichla ustulata	30	31	0.83	2.68	– 11.02	20
Hylocichla minima	20	32	0.83	2.59	– 13.01	20
Erithacus rubecula	25	18	0.68	3.78	7.35	2, 12, 13, 17, 19
Phoenicurus phoenicurus	1	15	0.46	3.07	– 17.31	13
Kittacincla macroura	1	25	0.90	3.60	12.45	2
Luscinia luscinia	5	18	0.67	3.72	5.77	2, 13, 14
Saxicola rubetra	5	15	0.58	3.87	4.26	13, 14
Sialia sialis	2	32	1.34	4.19	40.44	8
Timaliidae						
Garrulax leucolophus	2		2.55			22
Leiothrix lutea	1	16.5	1.07	6.48		2
Sylviidae						
Sylvia atricapilla	1	20	0.75	3.75	10.67	2
Sylvia communis	1	13	0.59	4.54	18.31	14
Sylvia borin	3	22	0.63	2.86	– 13.14	12, 14

Taxon	n	S	E	I_{rel}	Q_r	Author
Phylloscopus collybita	5	7	0.32	4.57	−0.29	5, 17
Phylloscopus trochilus	5	9	0.35	3.89	−8.81	5, 17
Locustella naevia	1	14	0.50	3.57	−4.89	17
Acrocephalus schoenobaenus	6	12	0.44	3.67	−6.60	17
Acrocephalus scirpaceus	5	13	0.48	3.69	−3.75	12
Regulidae						
Regulus regulus	11	5.5	0.36	6.55		1, 5, 10, 12, 14
Aegithalidae						
Aegithalos caudatus	17	8	0.45	5.63		5, 12, 16
Certhiidae						
Certhia familiaris	11	9	0.50	5.56		5, 12, 14
Sittidae						
Sitta europaea	12	22	1.06	4.82		5, 10, 12, 17
Paridae						
Parus major	41	16	0.86	5.38	−0.17	5, 12, 15, 19
Parus caeruleus	45	10	0.67	6.70	0.67	1, 5, 9, 12, 15, 19
Parus ater	14	9.5	0.66	6.95	2.00	5,16
Parus cristatus	4	10.5	0.70	6.67	2.40	16
Parus palustris	9	12	0.68	5.67	−7.56	5
Parus montanus	10	13	0.79	6.08	2.78	16
Nectariniidae						
Cyanomitra verticalis	1	10.5	0.52	4.95	7.69	6
Cinnyris coccinigaster	1	16	0.55	3.44	−7.18	6
Chalcomitra fuliginosa	1	7.2	0.43	5.97	6.98	5
Panaeola pulchella	1	6.25	0.35	5.60	−6.73	5
Oriolidae						
Oriolus oriolus	2	70	1.50	2.14		12
Cracticidae						
Gymnorhina tibicen	1		4.1			22
Corvidae						
Corvus corax	68	1150	15.3	1.33	−1.86	9, 10, 12, 15, 19, 22
Corvus albus	1		10.5			22
Corvus ruficollis	1		10.5			22
Corvus corone	67	470	8.5	1.81	−2.64	3, 4, 7, 9–14, 19, 22
Corvus frugilegus	19	440	7.9	1.80	−5.56	7, 12, 19, 22

Taxon	n	S	E	I_{rel}	Q_r	Author
Corvus monedula	13	200	4.8	2.40	−4.36	2, 3, 12, 13, 19, 22
Corvus brachyrhynchos	9	375	8.5	2.27	12.70	2, 15, 22
Corvus albicollis	1		12.0			22
Corvus "abyssinicus"	1		14.5			22
Corvus capensis	1		8.0			22
Urocissa erythrorhyncha	4		3.8			22
Cyanocorax chrysops	1		4.3			22
Cyanocorax yncas	2	60	2.4	4.00	4.34	2
Dendrocitta vagabunda	1		2.8			22
Cyanocitta cristata	3	80	3.0	3.75	8.24	2, 22
Cyanopica cyanea	1		3.0			22
Nucifraga caryocatactes	2	160	5.2	3.25	19.73	14, 22
Pyrrhocorax graculus	1	150	3.2	2.13	−23.17	10
Pyrrhocorax pyrrhocorax	2	300	5.9	1.97	−9.60	10, 12
Garrulus glandarius	28	170	4.2	2.47	−7.02	3, 4, 7, 12−14, 19, 22
Garrulus lidthi	1		4.3			22
Pica pica	21	210	6.2	2.95	19.70	4, 10, 12, 13, 22
Sturnidae						
Sturnus vulgaris	51	75	1.83	2.44		8, 9, 11, 12, 14, 19
Sturnus roseus	4	55	1.48	2.69		12
Ploceidae						
Passer domesticus	88	30	0.93	3.10	7.41	2, 8, 9, 12−14, 19−21
Passer montanus	6	25	0.71	2.84	−6.21	13
Passer griseus	3	32	0.97	3.03	6.82	6
Montifringilla nivalis	2	45	1.09	2.42	−6.63	12
Estrildidae						
Amandava amandava	9	6.2	0.39	6.29	17.58	2, 4
Lonchura malacca	1	10.8	0.56	5.19	16.66	2
Lonchura striata	2		0.77			4
Lonchura atricapilla	5	12.4	0.56	4.52	6.41	4
Poephila cincta	1	12	0.52	4.33	0.99	4
Estrilda astrild	1	8.0	0.35	4.38	−10.95	13

Taxon	n	S	E	I_{rel}	Q_r	Author
Estrilda troglodytes	1	5.6	0.36	6.43	16.15	4
Estrilda melpoda	1	7.5	0.35	4.67	−7.04	13
Spermestes cucullatus	3	8.5	0.39	4.59	−4.70	6, 13
Padda oryzivora	4	21	0.83	3.95	11.04	2
Taeniopygia guttata	1	11	0.43	3.91	−11.51	13
Amadina fasciata	1	15.5	0.55	3.55	−9.92	13
Pytilia phoenicoptera	1	7.7	0.37	4.81	−3.44	13
Steganura paradisea	1	16	0.55	3.44	−11.81	13
Fringillidae						
Fringilla coelebs	20	21	0.76	3.62	−11.24	9, 10, 12−14, 19
Fringilla montifringilla	3	24	0.85	3.54	−10.26	14, 19
Coccothraustes coccothraustes	8	50	1.63	3.26	−1.19	10, 12
Carduelis spinus	19	11	0.55	5.00	4.73	1, 12−14, 19
Carduelis carduelis	34	14	0.67	4.79	6.32	2, 4, 12−14, 19
Carduelis cannabina	18	17	0.70	4.12	−4.08	2, 4, 12−14, 19
Carduelis chloris	17	25	0.92	3.68	−5.82	13, 14, 19
Carduelis flammea	10	13	0.64	4.92	7.41	14
Serinus canaria	3	15	0.57	3.80	−14.14	4, 8, 13
Serinus serinus	3	9.5	0.48	5.05	2.12	13, 19
Loxia curvirostra	10	37	1.51	4.08	14.93	10, 12, 14
Loxia pytyopsittacus	2	56	1.82	3.25	1.27	14
Loxia leucoptera	1	35	1.20	3.43	−4.75	14
Pyrrhula pyrrhula	7	23	0.97	4.22	5.76	2, 4, 13, 14
Erythrina purpurea	1	20	0.85	4.25	3.01	2
Vireonidae						
Vireo olivaceus	13	19	0.59	3.11		18
Vireo philadelphicus	4	13	0.48	3.69		18
Parulidae						
Vermivora peregrina	16	9.9	0.39	3.94	0.41	20
Dendroica minima	33	8.4	0.39	4.64	14.49	20
Dendroica castanea	31	12.5	0.44	3.52	−5.98	20
Dendroica magnolia	18	8.8	0.38	4.32	7.49	18
Dendroica pennsylvanica	9	9.8	0.39	3.98	1.22	18
Seiurus aurocapillus	33	19	0.65	3.42	−0.60	20

Taxon	n	S	E	I_{rel}	Q_r	Author
Setophaga ruticilla	36	8.3	0.31	3.73	−8.12	20
Geothlypis trichas	12	11.8	0.47	3.98	5.17	18
Mniotilta varia	6	10.4	0.36	3.46	−10.89	18
Emberizidae						
Passerella melodia	1	21.5	0.88	4.09	6.60	2
Zonotrichia albicollis	1	32	1.07	3.34	−0.07	2
Junco hyemalis	1	18	0.86	4.78	17.01	2
Emberiza calandra	1	50	1.20	2.40	−16.30	13
Emberiza citrinella	2	30	0.85	2.83	−17.19	13, 14
Emberiza cirlus	1	25	0.79	3.16	−13.29	13
Emberiza schoeniclus	1	19	0.70	3.68	−8.07	14
Cardinalis cardinalis	1	44	1.45	3.30	9.96	2
Paroaria dominicana	3	26	1.16	4.46	24.09	2
Paroaria coronata	9	33	1.21	3.67	10.75	2, 4
Pheucticus ludovicianus	25	47	1.27	2.70	2.70	20
Icteridae						
Dolichonyx oryzivorus	9	40	0.95	2.38	−7.71	20
Sturnella magna	1	135	2.3	1.70	−39.79	2
Agelaius phoeniceus	1	70	1.77	2.53	−5.94	2
Erythropsar ruficapillus	1	33	0.81	2.45	−3.18	4
Quiscalus quiscula	1	82	2.92	3.56	30.84	8
Molothrus ater	1	66	2.69	4.08	52.31	8

1 = Welcker and Brandt 1903, 2 = Hrdlička 1905, 3 = Lapicque and Girard 1905, 4 = Girard 1908, 5 = Lapicque 1908, 6 = Waterlot 1912, 7 = Dosse 1937, 8 = Crile and Quiring 1940, 9 = Portmann and Sutter 1940, 10 = Portmann and Vischer 1943, 11 = Sutter 1943, 12 = Portmann 1947, 13 = Vaughien 1949, 14 = Skvorcova 1952, 15 = Spector 1956, 16 = Skvorcova 1956, 17 = Skvorcova 1961, 18 = Graber and Graber 1962, 19 = Senglaub 1963, 20 = Graber and Graber 1965, 21 = Ruprecht 1968, 22 = Mlíkovský this paper

In Emberizidae, brain size and body size are positively correlated (r_H = = 1.053 $\pm$ 0.316; $p < 0.05$) and their allometrical relation is $E = 0.111\ S^{0.654\pm0.126}$ (n = 11). The slope of this regression does not significantly differ from either the Dubois' constant ($t_s = 0.746$; $p > 0.05$) or the Jerison's constant ($t_s = -0.101$; $p > 0.05$).

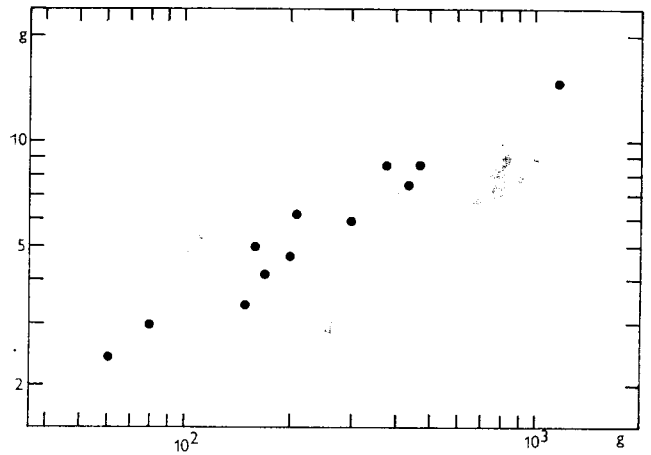
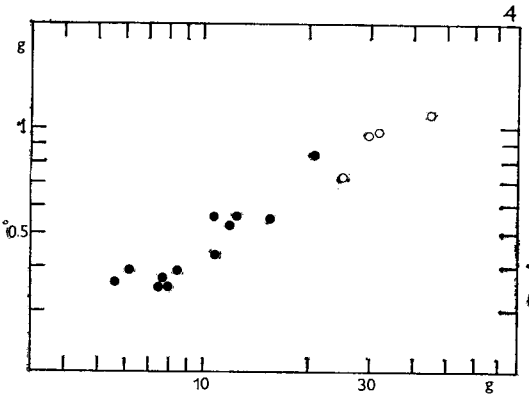


Fig. 3. Relationship between the brain size (Y axis) and the body size (X axis) in Corvidae. See Table 1 for exact data.

In Icteridae, brain size and body size are positively correlated ($r_s = 0.943$; $p < 0.05$) and their allometrical relation is $E = 0.0193\ S^{1.078\pm0.121}$ (n = 6). This appears totally unrealistic. A survey of the data revealed that encephalization values for the genera *Quiscalus* and *Molothrus* are markedly higher than those for the remaining 4 genera. It may be thus hypothesized that either



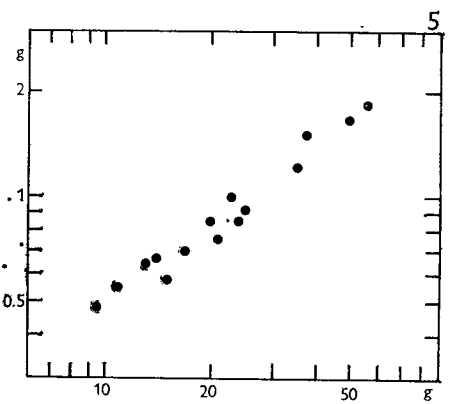


Fig. 4. Relationship between the brain size (Y axis) and the body size (X axis) in Ploceidae (○) and Estrildidae (●). See Table 1 for exact data.
Fig. 5. Relationship between the brain size (Y axis) and the body size (X axis) in Fringillidae. See Table 1 for exact data.

the family Icteridae is a heterogenous assemblage, which seems improbable, or that the values for *Quiscalus* and *Molothrus* (both were measured by Crile and Quiring 1940) are incorrect. More data on this family are needed to resolve this dilemma.

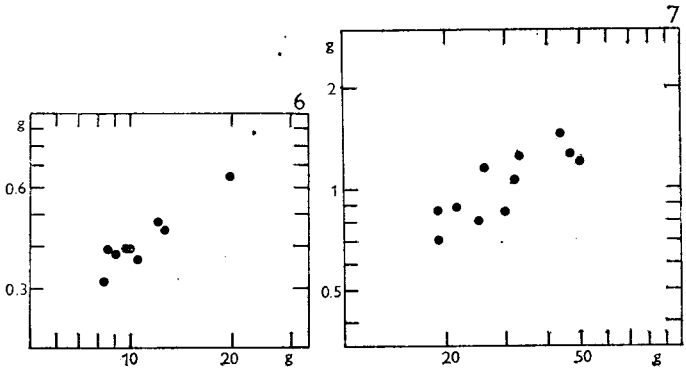


Fig. 6. Relationship between the brain size (Y axis) and the body size (X axis) in Parulidae. See Table 1 for exact data.
Fig. 7. Relationship between the brain size (Y axis) and the body size (X axis) in Emberizidae. See Table 1 for exact data.

SUMMARY

(1) A review of the brain size in birds and its relation to body size is presented. In general, data on 4344 brains in 766 extant species belonging to 116 families of birds are presented.

(2) The data were sufficient for the calculation of regression equations relating brain mass and body mass in 35 families of birds. The slopes of these regressions were found to vary between 0.440 in Trochilidae and 0.987 in Gaviidae. Higher values obtained for Threskiornithidae (a = 1.059) and Icteridae (a = 1.078) were discarded as statistical artifacts.

(3) The regression slopes were compared with the predicted Dubois' constant (a = 0.56). The slopes were found significantly higher than this constant in 10 families, significantly lower in 1 family (Alcidae) and deviating non-significantly (at p = 0.05 level) in 22 families. This indicates that the Dubois' rule is incorrect.

(4) The regression slopes were compared also with the predicted Jerison's constant (a = 2/3 = 0.667). The slopes were found significantly higher than this constant in 4 families, significantly lower in 12 families and deviating non-significantly in 17 families. This indicates that the Jerison's rule is incorrect.

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