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BRAIN SIZE IN BIRDS: 2. FALCONIFORMES THROUGH GAVIIFORMES

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Abstract. Brain size in 241 bird species and its relation to body size in 11 families of birds are estimated. The following avian orders are considered: Falconiformes, Galliformes, Gruiformes, Charadriiformes and Gaviiformes.

INTRODUCTION

This is a continuation of my review of the brain size in birds (Mlíkovský 1989). See the latter paper for the sections on Material and Methods.

RESULTS AND DISCUSSION

Falconiformes

The data on the brain size and the body size in Falconiformes are presented in Table 1 and Figures 1—2. The data were sufficient for the calculation of regression equations in the following falconiform families: Cathartidae, Accipitridae and Falconidae.

In Cathartidae, brain size and body size are positively correlated ($r_S = 1.000$; $p < 0.05$) and their allometrical relation is $E = 0.0406\ S^{0.732\pm0.0438}$ ($n = 4$). The slope of this regression is significantly higher than the Dubois' constant ($t_s = 3.927$; $p < 0.05$), but does not significantly differ from the Jerison's constant ($t_s = 1.492$; $p > 0.05$).

In Accipitridae, brain size and body size are positively correlated ($r_H = 2.265 \pm \pm 0.144$; $p < 0.001$) and their allometrical relation is $E = 0.169\ S^{0.553\pm0.0160}$ ($n = 49$). The slope of this regression is significantly lower than the Jerison's constant ($t_s = -7.104$; $p < 0.001$), but does not significantly differ from the Dubois' constant ($t_s = -0.438$; $p > 0.05$).

In Falconidae, brain size and body size are positively correlated ($r_H = 2.301 \pm \pm 0.258$; $p < 0.001$) and their allometrical relation is $E = 0.241\ S^{0.494\pm0.0232}$ ($n = 16$). The slope of this regression is significantly lower than both the Dubois' constant ($t_s = -2.845$; $p < 0.05$) and the Jerison's constant ($t_s = -7.443$; $p < 0.001$).

Galliformes

The data on the brain size and the body size in Galliformes are presented in Table 2 and Figure 3. The data were sufficient for the calculation of the regression equation in the family Phasianidae only.

In this family, brain size and body size are positively correlated ($r_H = 1.867 \pm \pm 0.162$; $p < 0.001$) and their allometrical relation is $E = 0.0951\ S^{0.528\pm0.0252}$

($n = 39$). The slope of this regression is significantly lower than the Jerison's constant ($t_s = -5.503$; $p < 0.001$), but does not significantly differ from the Dubois' constant ($t_s = -1.270$; $p > 0.05$).

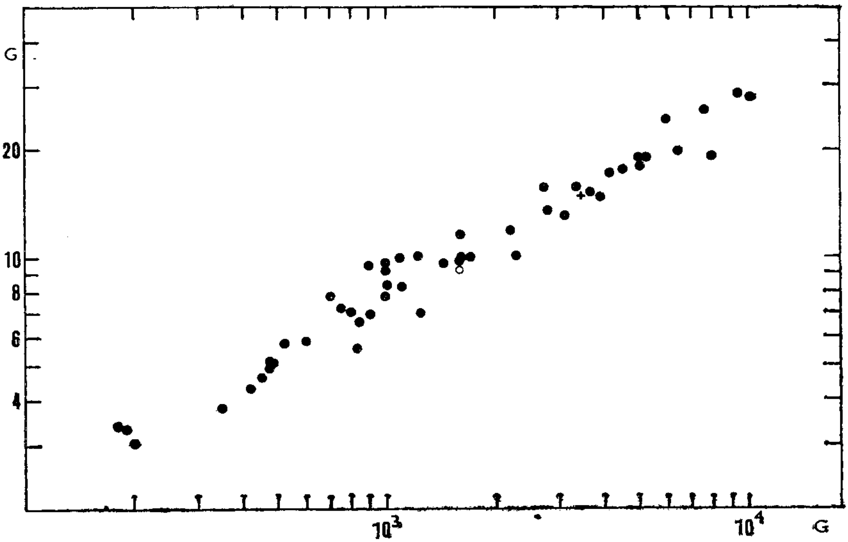


Fig. 1. Relationship between the brain size (Y yxis) and the body size (X axis) in Accipitridae (●) Pandion (○) and Sagittariidae (+). See Table 1 for exact data.

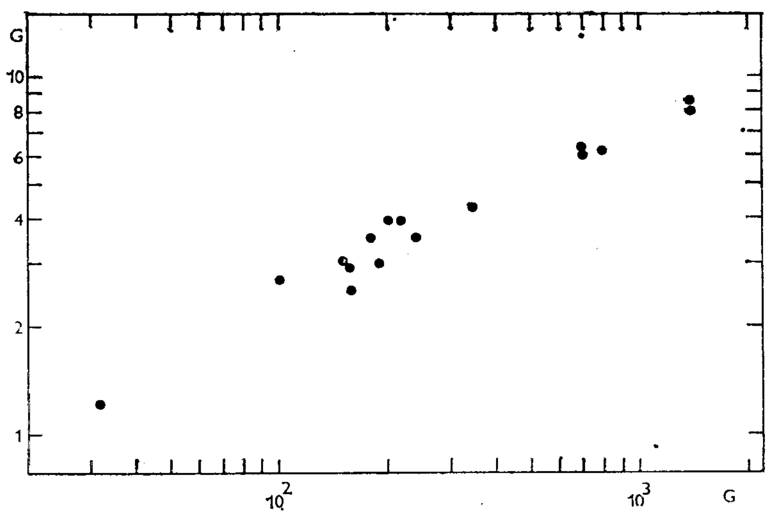


Fig. 2. Relationship between the brain size (Y axis) and the body size (X axis) in Falconidae. See Table 1 for exact data.

Table 1. Brain size and encephalization in Falconiformes

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 (1989) for the calculation of these indices. Author = who measured brains or cava cranii. The figure in parentheses after the family name gives number of extant species of that family (after Wolters 1975–1982).

Taxon	n	S	E	I_{rel}	Q_r	Author
Cathartidae (7)						
Coragyps atratus	2	1900	10.0	0.53	–1.95	13
Cathartes aura	7	1900	10.0	0 53	–1.95	1, 6, 13
Vultur gryphus	2	11000	35.3	0.32	–4.29	13
Sarcoramphus papa	2	4500	20.7	0.46	7.97	13
Accipitridae (225)						
Aegypius monachus	4	9500	27.3	0.29	2.00	8, 13
Gyps fulvus	2	7500	26.0	0.35	10.71	13
Gyps coprotheres	2	8000	19.0	0.24	–21.93	13
Gyps himalayensis	1	10000	28.0	0.28	1.69	13
Gyps benghalensis	1	5200	19.0	0.37	–0.94	13
Gyps africanus	1	6400	19.7	0.31	–8.43	6
Neophron percnopterus	4	2200	11.0	0.50	–7.71	13
Gypohierax angolensis	1	1700	10.0	0.59	–3.24	13
Gypaetus barbatus	6	6000	24.1	0.40	16.06	13
Haliaeetus albicilla	56	5000	19.0	0.38	1.24	13
Haliaeetus leucocephalus	2	5000	18.3	0.37	–2.49	13
Haliaeetus vociferus	1	3100	13.0	0.42	–9.77	13
Milvus milvus	4	1100	8.0	0.73	–1.53	12, 13
Milvus migrans	16	850	6.6	0.78	–6.31	4, 13
Pernis apivorus	3	750	7.2	0.96	9.53	13
Aviceda leuphotes	1	180	3.4	1.89	13.87	13
Accipiter gentilis	27	1000	7.8	0.78	1.21	8, 10, 13
Accipiter striatus	1	520	5.7	1.10	6.18	6
Accipiter nisus	19	200	3.0	1.50	–5.21	2, 3, 5, 7, 9, 10, 13
Accipiter tachiro	1	420	4.3	1.02	–9.86	13
Accipiter brevipes	1	190	3.3	1.74	7.27	13
Melierax canorus	3	900	6.8	0.76	–6.48	13
Kaupifalco monogrammicus	2	350	3.8	1.09	–11.89	13
Leucopternis schistacea	1		7.0			13
Buteogallus coronatus	1		4.6			13
Buteo magnirostris	2	480	4.9	1.02	–4.59	13
Buteo lineatus	2	800	7.0	0.88	2.75	1, 13
Buteo albicaudatus	1		15.0			13
Buteo jamaicensis	2	1100	9.9	0.90	21.86	6, 11
Buteo auguralis	1	1260	7.0	0.56	–20.07	13
Buteo rufofuscus	3	1000	9.5	0.95	23.26	13
Buteo rufinus	1	900	9.5	1.06	30.66	13
Buteo lagopus	6	1000	9.1	0.91	18.07	13
Buteo buteo	22	1000	8.2	0.82	6.40	2, 3, 6, 9, 10, 12, 13
Aquila audax	3	3400	15.2	0.45	0.24	13
Aquila chrysaetos	7	4500	17.6	0.39	–0.60	1, 8, 13
Aquila heliaca	1	2750	15.5	0.56	14.95	13
Aquila verreauxii	1	4200	17.0	0.40	–0.25	13
Aquila rapax	10	2800	14.0	0.50	2.79	6, 11
Aquila clanga	2	2200	11.8	0.54	–1.00	13
Aquila pomarina	4	1600	11.3	0.71	13.06	13
Lophaetus occipitalis	1	1450	9.0	0.62	4.91	13
Hieraaetus pennatus	1	820	5.5	0.67	–20.36	13

Table 1 — continuation

Taxon	n	S	E	I_{rel}	Q_r	Author
Nisaetus cirrhatus	1	2300	10.0	0.43	−18.14	13
Spizaetus ornatus	1	1215	10.0	0.82	16.50	13
Spizaetus melanoleucus	1		13.0			13
Butastur liventer	1	480	5.0	1.04	−2.65	13
Butastur teesa	1	480	4.9	1.02	−4.59	13
Dryotriorchis spectabilis	1		7.0			13
Circaetus cinereus	1	3900	14.5	0.37	−11.36	13
Circaetus fasciolatus	1		9.5			13
Spilornis cheela	1		8.0			13
Circus aeruginosus	8	600	5.8	0.97	−0.18	13
Circus cyaneus	8	450	4.6	1.02	−7.18	13
Polyboroides radiatus	3	700	7.7	1.10	21.69	13
Pandion haliaeetus	7	1600	9.6	0.60	−3.95	8, 13
Sagittariidae (1)						
Sagittarius serpentarius	1	3500	15.0	0.43		13
Falconidae						
Herpetotheres cachinnans	1	700	6.0	0.86	−2.13	13
Microhierax fringillarius	1	32	1.2	3.75	−10.13	13
Falco peregrinus	3	800	6.2	0.78	−5.32	13
Falco rusticolus	2	1400	8.0	0.57	−7.34	13
Falco biarmicus	1	700	6.3	0.90	2.76	13
Falco columbarius	7	190	3.0	1.58	−6.80	13
Falco sparverius	5	100	2.7	2.70	15.17	1, 6, 13
Falco naumanni	2	155	2.9	1.87	−0.38	13
Falco tinnunculus	11	200	3.8	1.90	15.10	7, 8, 12, 13
Falco moluccensis	1	180	3.5	1.94	11.67	13
Falco rupicoloides	1	240	3.9	1.63	7.95	13
Falco vespertinus	3	160	2.5	1.56	−15.46	13
Falco subbuteo	5	240	3.5	1.46	−3.12	13
Milvago chimango	1	350	4.3	1.23	−1.22	13
Polyborus plancus	1	1400	8.5	0.61	−1.55	13
Phalcobaenus albogularis	1	150	3.0	2.00	4.74	13

1 = Hrdlička 1905, 2 = Lapicque and Girard 1905, 3 = Girard 1908, 4 = Waterlot 1912, 5 = Dosse 1937, 6 = Crile and Quiring 1940, 7 = Portmann and Vischer 1943, 8 = Portmann 1947, 9 = Vaughien 1949, 10 = Skvorcova 1952, 11 = Spector 1956, 12 = Senglaub 1963, 13 = Mlíkovský this paper

Gruiformes

The data on the brain size and the body size in Gruiformes are presented in Table 3 and Figures 4—6. The data were sufficient for the calculation of regression equations in the following gruiform families: Rallidae, Gruidae and Otididae.

In Rallidae, brain size and body size are positively correlated ($r_H = 1.379 \pm \pm 0.333$; $p < 0.01$) and their allometrical relation is $E = 0.0639\ S^{0.659 \pm 0.0976}$ (n = 10). The slope of this regression does not significantly deviate from either the Jerison's constant ($t_s = -0.079$; $p > 0.05$) and the Dubois' constant ($t_s = 1.014$; $p > 0.05$). Remarkable is that the Fulicinae (*Gallinula* and *Fulica*) and *Crex* are markedly less encephalized than other rallids ($Q_r = -27.67$ to -16.55, and 4.60—32.88, respectively). It is improbable that this difference is caused by some measurement or other

Table 2. Brain size and encephalization in Galliformes. See Table 1 for explanation

Taxon	n	S	E	I_{rel}	Q_r	Author
Cracidae (43)						
Penelope superciliaris	1	1000	4.6	0.46		13
Crax alector	1		7.0			13
Opisthocomidae (1)						
Opisthocomus hoatzin	1	530	4.0	0.75		13
Megapodiidae (12)						
Leipoa ocellata	1		3.7			13
Phasianidae (203)						
Bonasa umbellus	1	500	2.7	0.54	6.69	1
Tetrastes bonasia	4	400	2.0	0.50	−11.09	13
Lagopus mutus	2	460	2.5	0.54	3.23	13
Lagopus lagopus	30	700	4.0	0.43	32.33	4, 11, 13
Lyrurus tetrix	8	1050	3.7	0.35	−1.18	8, 13
Tetrao urogallus	8	4500	6.0	0.13	−25.69	8, 13
Pavo cristatus	11	4000	6.7	0.17	−11.69	1, 2, 5, 7, 8, 13
Pavo muticus	1	4950	6.5	0.13	−23.44	13
Polyplectron bicalcaratum	2	600	3.1	0.52	11.25	13
Argusianus argus	1		5.4			13
Chrysolophus pictus	7	600	3.1	0.52	11.25	7, 8, 10, 13
Phasianus colchicus	532	1500	3.9	0.26	−13.72	2−5, 7, 8, 10, 12, 13
Lophura edwardsi	1		3.4			13
Gennaeus nycthemerus	3	1450	4.4	0.30	−0.90	8, 13
Crossoptilon crossoptilon	1	1850	6.1	0.33	20.80	13
Crossoptilon auritum	3	1750	5.9	0.34	20.32	13
Gallus gallus (wild)	3	850	3.2	0.38	−4.45	13
Gallus sonneratii	1	850	3.3	0.39	−1.46	13
Galloperdix spadicea	2	200	2.0	1.00	28.21	13
Tetraogallus himalayensis	3	1800	6.2	0.34	24.57	13
Perdix perdix	18	400	1.8	0.45	−19.98	5, 7, 8, 13
Alectoris graeca	4	600	2.1	0.35	−24.63	13
Alectoris rufa	4	335	2.0	0.60	−2.36	9, 13
Alectoris barbara	1	335	2.8	0.84	36.70	13
Bambusicola thoracica	2	400	1.8	0.45	−19.98	13
Francolinus leucoscepus	1	660	3.2	0.48	9.21	13
Francolinus swainsonii	1	600	3.8	0.63	36.38	13
Francolinus levaillantoides	1		2.7			13
Francolinus levaillantii	4	360	2.5	0.69	17.50	13
Francolinus sephaena	2	300	1.9	0.63	−1.68	4, 13
Francolinus pondicerianus	1	150	1.7	1.13	26.85	13
Ammoperdix heyi	1	190	1.5	0.79	−1.21	13
Coturnix coturnix	26	90	0.8	0.89	−21.82	5−9, 13
Excalfactoria chinensis	3	45	0.5	1.11	−29.55	13
Rollulus roulroul	1	165	1.9	1.15	34.82	13
Colinus virginianus	22	120	1.2	1.00	0.74	1, 13
Callipepla squamata	1	150	1.5	1.00	11.93	1
Callipepla californica	3	150	1.3	0.87	−3.00	1, 4
Guttera pucherani	1	1350	4.0	0.30	−6.45	13
Numida meleagris (wild)	8	1300	3.8	0.29	−9.33	1, 4, 9, 13

Table 2 — continuation

Taxon	n	S	E	I_{rel}	Q_r	Author
Meleagris ocellata	1	3500	5.8	0.17	−17.97	13
Meleagris gallopavo (wild)	3	4000	7.3	0.18	−3.78	13

1 = Hrdlička 1905, 2 = Lapicque and Girard 1905, 3 = Girard 1908, 4 = Crile and Quiring 1940, 5 = Portmann and Sutter 1940, 6 = Sutter 1943, 7 = Portmann and Vischer 1943, 8 = Portmann 1947, 9 = Vaughien 1949, 10 = Senglaub 1963, 11 = Sazikova 1975, 12 = Werner 1975, 13 = Mlíkovský this paper

error(s). Encephalization needs to be studied in more rallid species before an explanation of this phenomenon can be found.

In Gruidae, brain size and body size are positively correlated ($r_S = 0.946$; $p < 0.01$) and their allometrical relation is $E = 0.0192\ S^{0.788 \pm 0.0441}$ ($n = 8$). The slope of this regression is significantly higher than both the Jerison's constant ($t_s = 2.751$; $p < 0.05$) and the Dubois' constant ($t_s = 5.170$; $p < 0.01$).

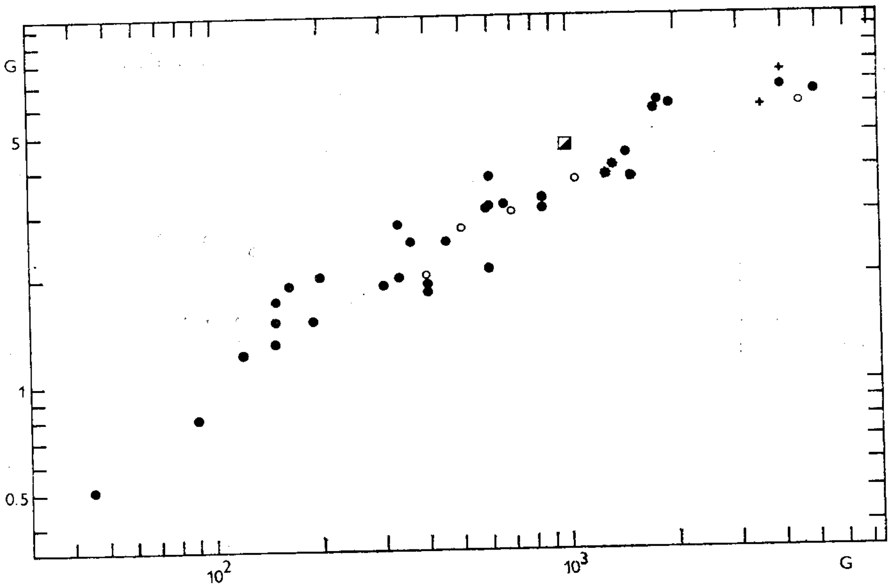
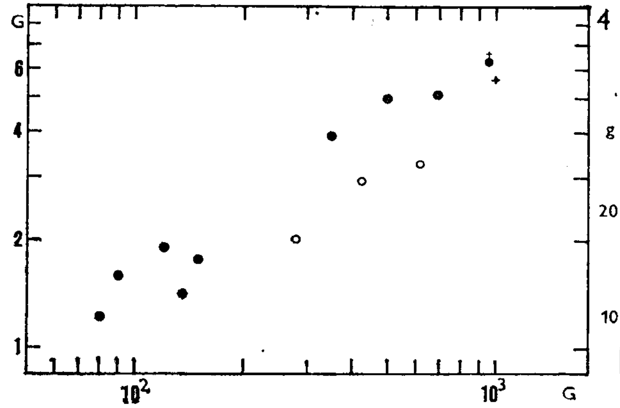


Fig. 3. Relationship between the brain size (Y axis) and the body size (X axis) in Galliformes. ○ = Tetraoninae, ∗ = Numidinae, + = Meleagrinae, ● = other Phasianidae, □ = Cracidae. See Table 2 for exact data.

In Otididae, brain size and body size are positively correlated ($r_S = 1.000$; $p < 0.01$) and their allometrical relation is $E = 0.157\ S^{0.493 \pm 0.0503}$ ($n = 5$). The slope of this regression is significantly lower than the Jerison's constant ($t_s = -3.453$; $p < 0.05$), but does not significantly differ from the Dubois' constant ($t_s = -1.332$; $p > 0.05$).



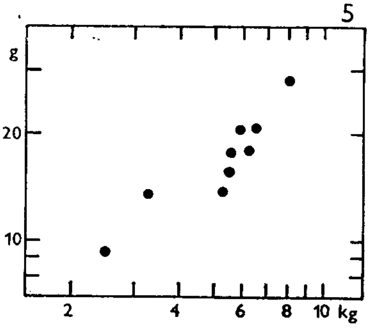
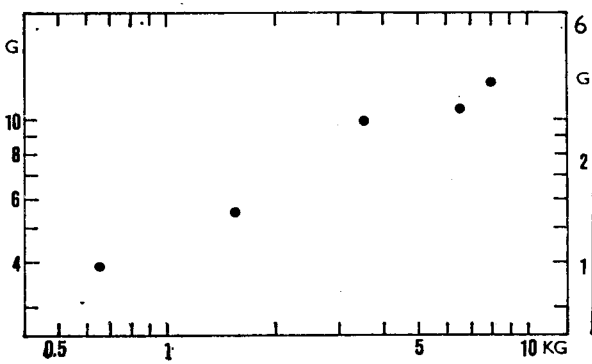


Fig. 4. Relationship between the brain size (Y axis) and the body size (X axis) in Rallidae (●; ○ = Fulicinae), Heliornithidae (*), Aramidae (♀) and Psophiidae (+). See Table 3 for exact data.

Fig. 5. Relationship between the brain size (Y axis) and the body size (X axis) in Gruidae. See Table 3 for exact data.



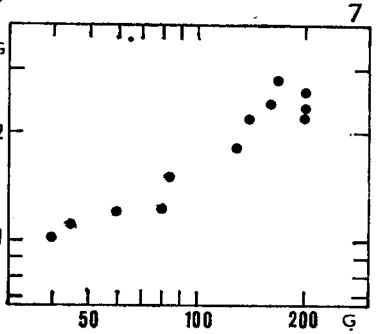


Fig. 6. Relationship between the brain size (Y axis) and the body size (X axis) in Otididae. See Table 3 for exact data.

Fig. 7. Relationship between the brain size (Y axis) and the body size (X axis) in Charadriidae. See Table 4 for exact data.

Charadriiformes

The data on the brain size and the body size in Charadriiformes are presented in Table 4 and Figures 7—10. The data were sufficient for the calculation of regression equations in the following charadriiform families: Charadriidae, Scolopacidae, Laridae and Alcidae.

In Charadriidae, brain size and body size are positively correlated ($r_H = 1.743 \pm \pm 0.302$; $p < 0.001$) and their allometrical relation is $E = 0.0938\ S^{0.624 \pm 0.0584}$ ($n = 12$). The slope of this regression does not significantly deviate from either the Jerison's constant ($t_s = -0.731$; $p > 0.05$) and the Dubois' constant ($t_s = 1.096$; $p > 0.05$).

Table 3. Brain size and encephalization in Gruiformes.
See Table 1 for explanation

Taxon	n	S	E	I_{rel}	Q_r	Author
Rallidae (127)						
Crex crex	5	150	1.4	0.93	−19.35	5
Rallus aquaticus	21	120	1.6	1.38	10.10	5, 7, 9
Gallirallus australis	2	700	5.1	0.73	6.45	9
Aramides cajanea	1	350	3.9	1.11	28.54	9
Porzana porzana	9	80	1.2	1.50	4.60	5, 6, 9
Limnocorax flavirostris	6	90	1.6	1.78	29.05	2, 9
Tribonyx mortierii	2		4.2			9
Porphyrio porphyrio	6	500	5.1	1.02	32.88	4, 5, 9
Gallinula chloropus	7	280	2.0	0.71	−23.64	1, 5, 9
Fulica americana	1	430	2.9	0.67	−16.55	9
Fulica atra	21	650	3.3	0.51	−27.67	1, 5, 9
*Montirallus gypsorum**	1		3.1			8
Heliornithidae (1)						
Heliornis fulica	1	135	1.4	1.04		9
Rhynochetidae (1)						
no data						
Eurypygidae (1)						
Eurypyga helias	1		2.7			9
Mesoenatidae (3)						
no data						
Turnicidae (16)						
Turnix sylvatica	2		0.6			9
Turnix nigricollis	1		0.9			9
Pedionomidae (1)						
no data						
Gruidae (14)						
Grus antigone	5	8000	20.6	0.26	−9.86	5, 9
Grus grus	4	5500	17.6	0.32	3.47	9
Grus japonensis	3	6500	20.7	0.32	6.68	9
Grus canadensis	1	5500	15.5	0.28	−8.88	3
Grus leucogeranus	1	5900	20.5	0.35	14.03	9
Tetrapteryx paradisea	3	5300	13.3	0.25	−19.50	9
Anthropoides virgo	7	2500	9.4	0.38	2.86	5, 9
Balearica pavonina	10	3250	13.7	0.42	21.91	3, 5, 9
Aramidae (1)						
Aramus guarauna	2	950	6.3	0.66		9
Psophiidae (3)						
Psophia crepitans	3	1000	5.7	0.57		1, 9
Psophia leucoptera	1		5.2			9
Cariamidae (2)						
Chunga burmeisteri	1		7.5			9

Table 3 — continuation

Taxon	n	S	E	I_{rel}	Q_r	Author
Otididae (22)						
Chlamydotis undulata	1	1550	5.5	0.35	−6.32	9
Otis tarda	19	6600	10.8	0.16	−9.95	9
Ardeotis arabs	1	3500	10.0	0.29	13.99	9
Ardeotis kori	4	8000	13.4	0.17	1.62	3, 9
Eupodotis cafra	1		4.2			9
Eupodotis afra	2	650	3.9	0.60	1.95	9
Eupodotis vigorsii	1		3.4			9

* Eocene species (see Mlíkovský 1981 for its taxonomic position)
1 = Girard 1908, 2 = Waterlot 1912, 3 = Crile and Quiring 1940, 4 = Portmann and Vischer 1943, 5 = Portmann 1947, 6 = Skvorcova 1952, 7 = Sigmund 1958, 8 = Jerison 1973, 9 = Mlíkovský this paper

In Scolopacidae, brain size and body size are positively correlated ($r_H = 2.176 \pm \pm 0.213$; $p < 0.001$) and their allometrical relation is $E = 0.0912\ s^{0.587 \pm 0.0263}$ ($n = 23$). The slope of this regression is significantly lower than the Jerison's constant ($t_s = -3.029$; $p < 0.01$), but does not significantly deviate from the Dubois' constant ($t_s = 1.027$; $p > 0.05$).

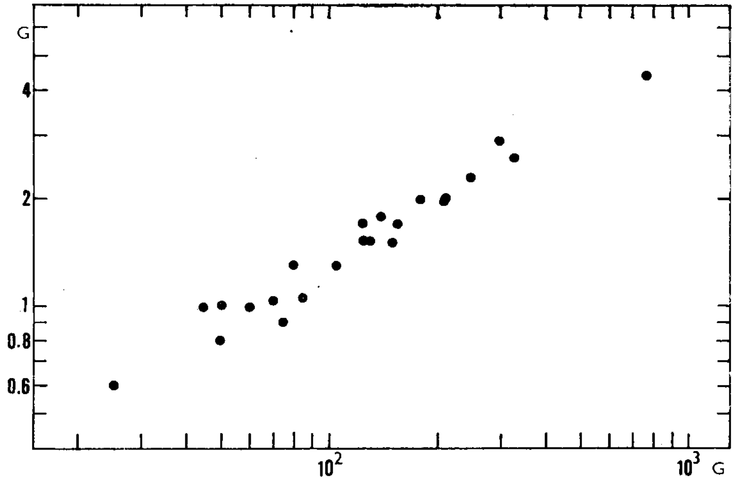


Fig. 8. Relationship between the brain size (Y axis) and the body size (X axis) in Scolopacidae. See Table 4 for exact data.

In Laridae, brain size and body size are positively correlated ($r_H = 2.134 \pm \pm 0.224$; $p < 0.001$) and their allometrical relation is $E = 0.117\ s^{0.577 \pm 0.0283}$ ($n = 21$). The slope of this regression is significantly lower than the Jerison's constant ($t_s = -3.168$; $p < 0.01$), but does not significantly deviate from the Dubois' constant ($t_s = 0.601$; $p > 0.05$).

Table 4. Brain size and encephalization in Charadriiformes. See Table 1 for explanation

Taxon	n	S	E	I_{rel}	Q_r	Author
Jacanidae (8)						
Actophilornis africanus	3	125	1.5	1.20		4, 11
Rostratulidae (2)						
Rostratula benghalensis	1	100	1.4	1.40		11
Haematopodidae (8)						
Haematopus ostralegus	7	550	3.9	0.71		7, 11
Haematopus longirostris	1		4.4			11
Ibidorhynchidae (1)						
no data						
Recurvirostridae						
Recurvirostra avocetta	2	340	2.0	0.59		11
Dromadidae (1)						
Dromas ardeola	3	280	3.9	1.39		11
Burhinidae (9)						
Burhinus capensis	2	430	3.8	0.88		11
Burhinus oedicnemus	7	400	3.5	0.88		7, 11
Burhinus bistriatus	1		4.3			11
Glareolidae (17)						
Rhinoptilus chalcopterus	3		1.5			11
Cursorius cursor	1		1.3			11
Cursorius temminckii	1		1.3			11
Charadriidae (65)						
Microsarcops cinereus	1	170	2.8	1.65	21.10	11
Stephanibix coronatus	3	140	2.2	1.57	7.41	11
Belonopterus cayenensis	1	160	2.4	1.50	7.80	11
Vanellus vanellus	11	200	2.2	1.10	−14.02	6, 7, 9, 11
Pluvialis apricaria	1	200	2.3	1.15	−10.12	11
Pluvialis dominica	1	130	1.8	1.38	−7.96	11
Pluvialis squatarola	6	200	2.6	1.30	1.61	8, 11
Charadrius leschenaultii	1	85	1.5	1.76	−0.02	11
Charadrius vociferus	1	80	1.2	1.50	−16.93	1
Charadrius dubius	1	40	1.0	2.50	6.69	11
Charadrius hiaticula	7	60	1.2	2.00	−0.59	8, 11
Charadrius alexandrinus	1	45	1.1	2.44	9.04	11
Charadrius tricollaris	2		1.0			11
Scolopacidae (85)						
Philohela minor	1	105	1.3	1.24	−7.21	11
Scolopax rusticola	19	330	2.6	0.79	−5.24	3, 6−9, 11
Philomachus pugnax	11	155	1.7	1.10	−3.46	7, 8, 11
Calidris canutus	1	150	1.5	1.10	−13.16	11
Calidris ferrugineus	2	75	0.9	1.20	−21.73	8
Calidris minutus	3	25	0.6	2.40	−0.56	8, 11
Calidris alpinus	6	45	1.0	2.22	17.37	8, 11
Calidris maritimus	2	80	1.3	1.63	8.85	11
Gallinago gallinago	14	130	1.6	1.23	0.75	3, 7, 8, 11

Table 4 — continuation

Taxon	n	S	E	I_{rel}	Q_r	Author
Gallinago media	2	210	2.1	0.95	−0.21	11
Lymnocryptes minimus	9	60	1.0	1.67	−0.86	7, 8, 11
Limosa limosa	2	300	2.9	0.97	11.77	11
Limosa lapponica	2	250	2.3	0.92	−1.34	11
Numenius arquata	8	760	4.3	0.57	−3.96	3, 7, 11
Numenius tahitiensis	1		3.7			10
Numenius phaeopus	1	480	4.7	0.98	37.47	11
Tringa erythropus	2	140	1.8	1.29	8.52	11
Tringa totanus	3	125	1.7	1.36	9.54	11
Tringa nebularia	2	180	2.0	1.11	−4.04	11
Tringa melanoleuca	1	210	2.0	0.95	−4.96	11
Tringa glareola	4	70	1.2	1.71	8.67	8, 11
Tringa ochropus	3	85	1.3	1.53	5.05	11
Tringa solitaria	2	50	1.0	2.00	10.33	11
Actitis hypoleucos	10	50	0.8	1.60	−11.73	8, 9, 11
Arenaria interpres	2	125	1.5	1.20	−3.35	11
Thinocoridae (4)						
Thinocorus orbignyianus	1	135	1.2	0.89		11
Chionididae (2)						
Chionis minor	3	430	3.6	0.84		11
Pterocletidae (16)						
Syrrhaptes paradoxus	3	300	1.6	0.53		11
Syrrhaptes orientalis	2	510	2.4	0.47		11
Syrrhaptes gutturalis	1		1.5			11
Syrrhaptes exustus	1		1.4			11
Pterocles coronata	1		1.4			11
Stercorariidae (4)						
Stercorarius kua	1	800	7.5	0.94		11
Laridae (85)						
Larus canus	9	450	4.1	0.91	3.20	9, 11
Larus glaucoides	1	900	7.5	0.83	26.55	11
Larus fuscus	1	870	5.7	0.66	−1.92	11
Larus argentatus	13	1130	6.6	0.58	−2.34	1, 2, 5, 7−9, 11
Larus marinus	4	1660	7.9	0.48	−6.36	7, 11
Larus dominicanus	1	1000	5.9	0.59	−6.32	11
Larus hyperboreus	1	1400	8.0	0.57	4.61	11
Larus hemprichii	1	470	2.9	0.62	−28.81	11
Larus leucophthalmus	3	320	3.2	1.00	−1.94	11
Larus ridibundus	22	300	2.85	0.95	−9.35	6−9, 11
Larus philadelphia	1	220	2.5	1.14	−4.90	5
Larus atricilla	3	300	3.2	1.07	1.78	11
Larus minutus	1	125	1.9	1.52	0.15	11
Rissa tridactyla	2	410	3.8	0.93	0.93	11
Chlidonias leucoptera	2	65	1.4	2.15	7.62	11
Sterna sandvicensis	2	250	2.8	1.12	−1.06	11
Sterna sumatrana	1	95	2.0	2.11	23.51	11
Sterna hirundo	3	135	1.7	1.26	−14.28	7, 11
Sterna paradisea	2	110	2.0	1.82	13.49	9, 11
Sterna albifrons	2	40	0.9	2.25	−8.45	9, 11
Phaetusa simplex	2	220	3.2	1.45	21.73	11

Rynchopidae (3)						
Rynchops niger	1	290	2.0	0.69		11
Alcidae (22)						
Cepphus grylle	4	430	3.2	0.74	−13.12	11
Uria aalge	3	1050	5.3	0.50	−3.63	5, 11
Uria lomvia	1	990	5.1	0.52	−4.78	11
Alca torda	5	720	4.9	0.68	5.55	11
*Pinguinus impennis**	1	5000	10.5	0.21	−5.26	11
Alle alle	1	100	1.9	1.90	−0.70	5
Fratercula arctica	5	490	4.4	0.90	12.65	7, 11
Lunda cirrhata	1	980	5.9	0.60	10.66	11

* Extinct species
1 = Hrdlička 1905, 2 = Lapicque and Girard 1905, 3 = Girard 1908, 4 = Waterlot 1912, 5 = Crile and Quiring 1940, 6 = Portmann and Vischer 1943, 7 = Portmann 1947, 8 = Skvorcova 1952, 9 = Senglaub 1963, 10 = Jerison 1973, 11 = Mlíkovský this paper

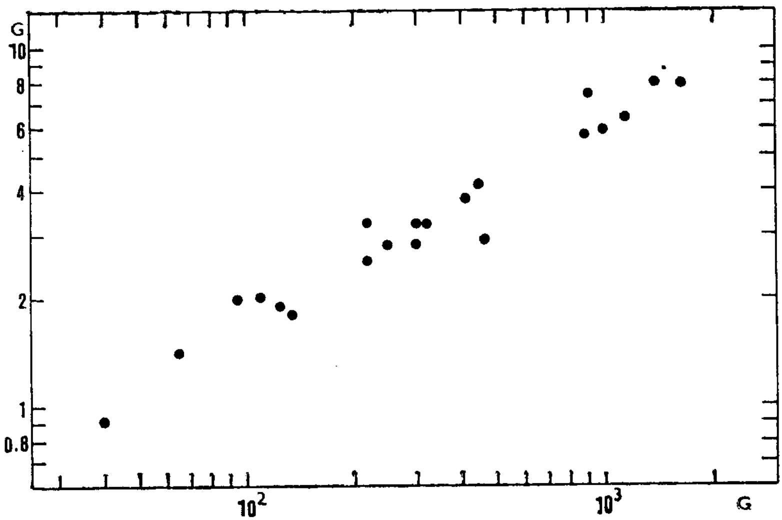


Fig. 9. Relationship between the brain size (Y axis) and the body size (X axis) in Laridae. See Table 4 for exact data.

Table 5. Brain size and encephalization in Gaviiformes. See Table 1 for explanation

Taxon	n	S	E	I_{rel}	Q_r	Author
Gaviidae (5)						
Gavia stellata	5	1600	5.3	0.33		1−3
Gavia arctica	10	2500	7.5	0.30		3
Gavia immer	2	4000	13.0	0.33		3

1 = Crile and Quiring 1940, 2 = Portmann 1947, 3 = Mlíkovský this paper

In Alcidae, brain size and body size are positively correlated ($r_S = 0.929$; $p < 0.01$) and their allometrical relation is $E = 0.242\ S^{0.449 \pm 0.00326}$ ($n = 8$). The slope of this regression is significantly lower than both the Jerison's constant ($t_s = -6.677$; $p < 0.001$) and the Dubois' constant ($t_s = -3.405$; $p < 0.01$).

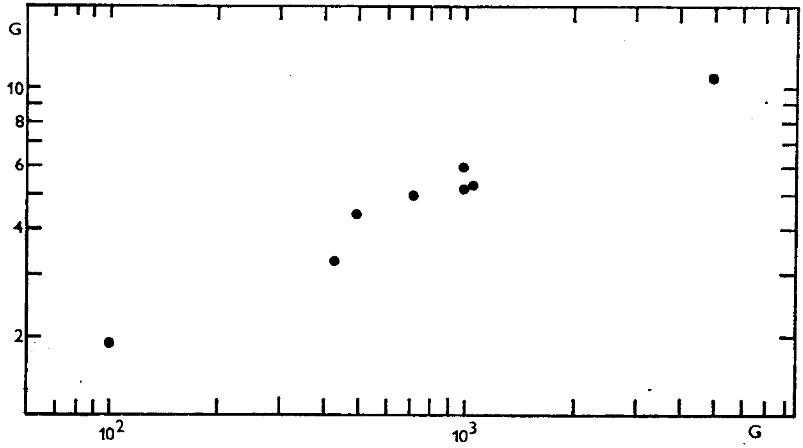


Fig. 10. Relationship between the brain size (Y axis) and the body size (X axis) in Alcidae. See Table 4 for exact data.

Gaviiformes

The data on the brain size and the body size in Gaviiformes are presented in Table 5. The data do not allow the calculation of the regression equation for the Gaviidae, the only living gaviiform family.

REFERENCES

Crile, G., D. P. Quiring, 1940: A record of the body weight and certain organ and gland weight in 3690 animals. *Ohio J. Sci.*, 40 219—259.

Dosse, G., 1937: Vergleichende Gewichtsuntersuchungen am Vogelskelett. *Zool. Jb. Anat.*, 63:299—350.

Girard, P., 1908: Facteurs dont dependent la masse, la forme et la composition chimique quantitative de l'encéphale chez les oiseaux. Paris: Épinal, 68 pp.

Hrdlička, A., 1905: Brain weight in vertebrates. *Smithson. misc. Coll.*, 48: 89—112.

Jerison, H. J., 1973: Evolution of the brain size and intelligence. New York: Academic Press, xiv + 482 pp.

Lapicque, L., P. Girard, 1905: Poids de l'encéphale au fonction du poids du corps chez les oiseaux. *C. R. Acad. Sci. Paris*, 140: 1057—1059.

Mlíkovský, J., 1981: Relationships of the Eocene bird "Numenius" gypsorum Gervais. *Bull. Mus. natl. Hist. nat.*, 4, C, 3:'341—343.

Mlíkovský, J., 1989: Brain size in birds: 1. Tinamiformes through Ciconiiformes. *Věst. čs. Společ. zool.*, *53*: 33—47.

Portmann, A., 1947: Etudes sur la cérébralisation chez les oiseaux. II. Les indices intercérébraux. *Alauda*, 15: 1—15.

Portmann, A., E. Sutter, 1940: Über die postembryonale Entwicklung des Gehirns bei Vögeln. *Rev. suisse Zool.*, 47 : 195—202.

Portmann, A., L. Vischer, 1943: Organgewichte bei Vögeln. *Rev. suisse Zool.*, 50: 277—282.

Sazikova, T. G., 1975: Vozrastnaja izmenčivosť nekotorych morfologičeskich priznakov u dikich i domašnich ptic (Ontogenetic changes of some morphological characters in wild and domestic birds). In: V. N. Pavlinin, ed., Populjacionnaja izmenčivosť životnych (The population variability of animals): 139—142. Sverdlovsk: AN SSSR.

Senglaub, K., 1963: Das Kleinhirn der Vögel in Beziehung zu phylogenetischer Stellung, Lebensweise und Körpergrösse, nebst Beiträge zum Domestikationsproblem. *Z. wiss. Zool.*, 169: 1—63.

Sigmund, L., 1958: Postembryonální vývoj chřástala vodního (Rallus aquaticus) (Postembryonal development of the Water Rail (Rallus aquaticus)). *Sylvia*, 15: 85—118.

Skvorcova, T. A., 1952: Veličina i osobennosti stroenija mozga nekotorych vidov ptic v sootnošenii s drugimi organami i v svjazi s obrazom žizni i dvigateľnoj aktivnosťju (Brain size and peculiarities of the brain structure in some bird species in relation to other organs and in connection with life habits and locomotor activity). Unpublished Ph. D. Thesis, Leningrad, Leningrad State University.

Spector, W. S., ed., 1956: Handbook of biological data. Philadelphia: Saunders, xxxv + 584 pp.

Sutter, E., 1943: Über das embryonale und postembryonale Hirnwachstum bei Hühnern und Sperlingsvögeln. *Denkschr. schweiz. naturforsch. Ges.*, 75: 1—110.

Vaughien, L., 1949: Sur le poids relatif de l'encéphale des Oiseaux. *C. R. Acad. Sci. Paris*, 228: 711—713.

Waterlot, G., 1912: Détermination de poids encéphalique et de grandeur oculaires chez quelques vertébrés du Dahomey. *Bull. Mus. natl. Hist. nat.*, 1912: 491—494.

Werner, U., 1975: Vergleiche von Gehirngewicht und Körpergewicht bei Fasanen aus Volierenzuchten und aus der freien Wildbahn. Unpublished Thesis, Hannover, Tierärztliche Hochschule, 67 pp.

Wolters, H. E., 1975—1982: Die Vogelarten der Erde. Hamburg: Paul Parey, xx + 748 pp.

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