SCALING OF SKELETAL MASS TO BODY MASS IN BIRDS AND MAMMALS

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Animal skeletons scale allometrically with body mass, so that skeletons of large animals are proportionately more massive than those of small animals. The comparison of this allometry between birds and mammals is of interest because of the commonly held notion that birds have proportionately lighter skeletons as an adaptation for flight (e.g., Van Tyne and Berger 1966; Villee et al. 1973; Hickman et al. 1974; Welty 1975). Differences in skeletal mass and other specializations for flight, such as pneumatization, should be manifested in differences of the scaling of individual bones relative to body mass. These, in turn, may give clues to the mechanical constraints which operated in the evolution of flight.

The skeletal mass of mammals as a function of body mass has been described by Kayser and Heusner (1964), but their analysis is based upon only seven values. We have found that their allometric equation tends to overestimate skeletal mass for small mammals. Data which describe the scaling of avian skeletal mass were not available.

To provide a better founded allometric relationship for mammals and to allow comparison with the relative skeletal mass of birds, we have collected additional data on mammals and measured the masses of avian skeletons for a wide range of body masses. From these data we have derived new equations which describe the allometry of skeletal mass to body mass. Further, we have examined the scaling of avian long bones and attempted to analyze the mechanical consequences of our findings.

MATERIALS AND METHODS

For our analysis of mammals we collected data from Heusner (1963), Ziegler (1973), Ultsch (1974) and Wing (personal communication). These were analyzed for the least-squares logarithmic regression line which described the allometry of skeletal mass to body mass. The combined data consist of 49 values which represent 29 species, 18 families and nine orders. The range of body mass included in the sample

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was 0.006–6,600 kg. The range of skeletal mass was 0.0003–1,782 kg. The data and the identity of the specimens are given in Appendix A.

Data on the avian skeletons were taken from 311 specimens which represent 209 species, 73 families, and 27 orders. The majority of the specimens were obtained from the collections of P. Brodkorb and K. C. Campbell, who had the foresight to record the fresh body masses of their specimens before preparation of the skeletons. Data on two species were obtained from Ziegler (1973), and the body masses of 12 specimens for which no data had been recorded were estimated from Schönwetter (1960–1972). The dry skeletal masses were measured on one of several laboratory balances with a range appropriate to the mass of the skeleton. Preparation of the skeletons was by bacterial maceration or dermistid cleaning. There was no apparent difference between the two methods of preparation in our samples. The range of body masses included in the avian data is 0.0031–80.92 kg. Skeletal masses ranged 0.00088–7.72 kg. These data and the identity of the specimens are given in Appendix B.

A subset of the bird specimens was used for measurement of dimensions of the long bones. This group was selected by choosing 22 specimens as near as possible to regular logarithmic intervals of the range of body mass without regard to the identity or any other characteristic of the specimen. The skeletal mass/body mass allometry of the subset was within the 99% confidence interval of that for the whole sample and had a correlation coefficient of .997. Length of the long bones was measured between the bearing surfaces at either end. Width was measured at the midpoint of the shaft across a diameter which was parallel with the anterior-posterior axis of the animal. Measurements of length and thickness were made with a meter stick, vernier calipers, or a microscopic comparator, whichever was appropriate to the bone in question. The data for the avian subset are given in Appendix C.

RESULTS AND DISCUSSION

Skeletal Mass Allometry

The allometry of skeletal mass to body mass for our sample of mammals is shown in figure 1. The allometric equation we have calculated, Skeletal mass, kg $= 0.061$ (Body mass, kg)$^{1.090}$, differs from that from Kayser and Heusner (1964), (Skeletal mass, kg $= 0.093$ (Body mass)$^{1.142}$), in that both the slope of the logarithmic regression line and the intercept are lower in our analysis. These differences compensate for the overestimates we found from their allometric equation.

The skeletal mass/body mass allometry for birds is shown in figure 2. The allometric equation calculated from these data is Skeletal mass, kg $= 0.065$ (Body mass, kg)$^{1.071}$. As in the case of the mammals the skeletal mass is proportionately larger for larger animals. The slopes for the logarithmic regression lines for mammals and birds (1.090 and 1.071, respectively) are very nearly the same. If avian skeletons were proportionately lighter than those of mammals then the elevation of the regression line from the bird data, as indicated by the intercept, should be smaller than that from the mammal data, and hence lower on a graph. In fact, the intercept values for the mammalian and avian lines (0.061 and 0.065, respectively) are nearly

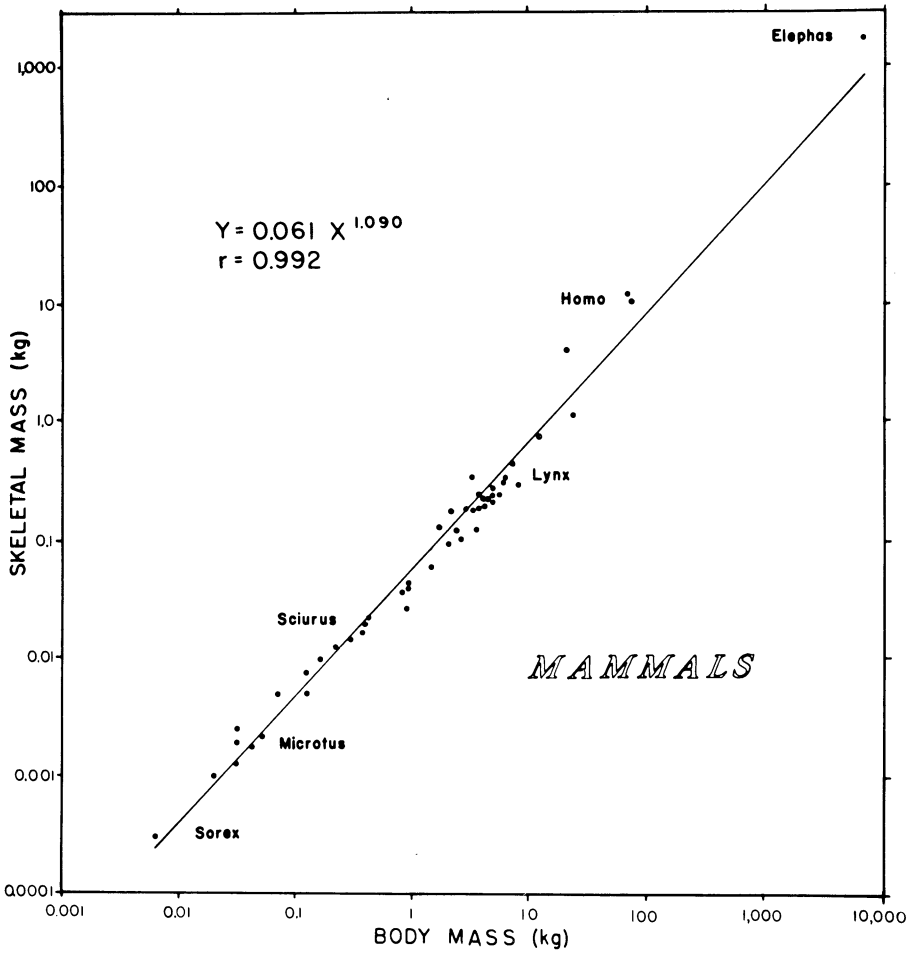

FIG. 1.—Relationship between skeletal mass (y) and body mass (x) for mammals. The sample for the logarithmic regression consisted of 49 data; the standard error of estimate for y on x was 0.154; the range of body mass values included in the sample was 0.006–6,600 kg. Examples of representative animals are listed with their genus name on a line intersecting their skeletal mass.

identical. An analysis of covariance indicates that neither the slopes nor the elevations differ significantly at the 0.01 level. Thus, contrary to common expectations, the skeletons of birds are not lighter than those of mammals.

It has been presumed that the air-filled (pneumatized) condition of some avian long bones together with their thinner walls was a mechanism by which a relative weight saving in the avian skeleton was achieved. If there is no weight saving, as we have shown, then the functional significance of pneumatization remains to be explained.

The hypothesis that pneumatization may serve as an energy saving from the reduction of the oscillating mass of the wing is questionable; the mass of fluid or tissue which might fill the lumen of a wing bone is probably very small relative to the

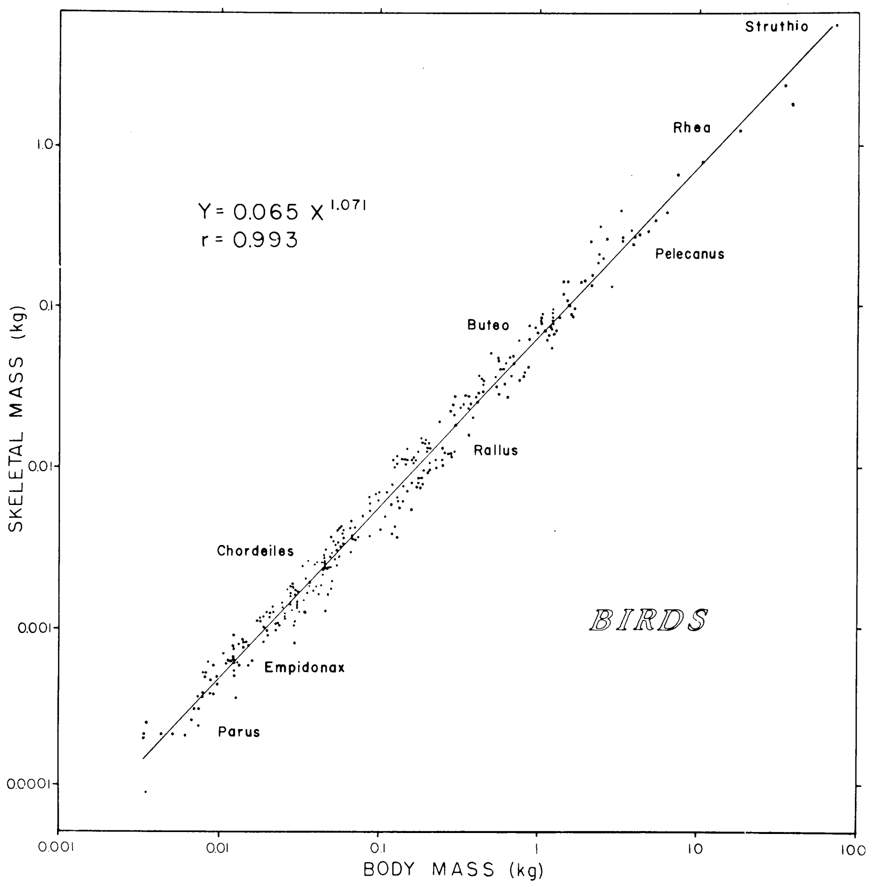

FIG. 2.—Relationship between skeletal mass (y) and body mass (x) for birds. The sample for the logarithmic regression consisted of 311 data; the standard error of estimate for y on x was 0.102; the range of body mass values included in the sample was 0.0031–80.920 kg. Examples of representative animals are listed with their genus name on a line intersecting their skeletal mass.

mass of the feathers. Brodkorb (1955) reports that the contour feathers alone of a bald eagle amounted to 14% of the body mass while the entire skeleton was not quite 7%.

Dimensional Allometry of Avian Long Bones

Our findings on the overall similarity of the skeletal mass allometry of birds and mammals led us to consider the functions and dimensional relationships of the long bones of the avian skeleton. The scaling of length and width for long bones of most animals departs from geometric similarity in that the bones become relatively thicker as they become longer. That is, width is generally proportional to length raised to a power greater than one (positive allometry). For example, for the avian femurs and tibiotarsi in our study, width is proportional to length raised to the 1.13 power. The width of long bones for several families of adult ungulates (McMahon 1975) scales to length raised to powers 1.04–2.42. This trend in allometry is consistent with what one

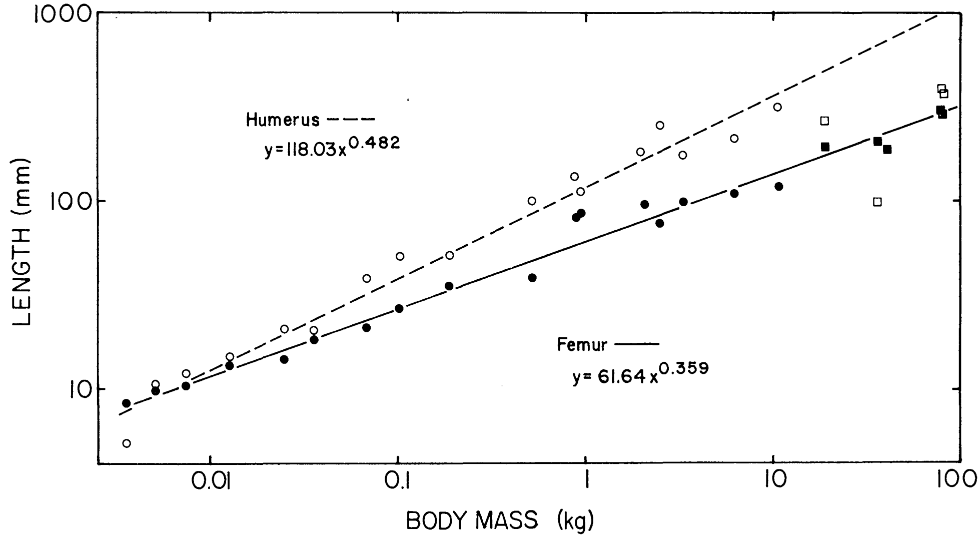

FIG. 3.—Relationship between the length (y) of avian femur and humerus and body mass (x). Open symbols (○, □) refer to the humerus; solid symbols (●, ■) refer to the femur; circular symbols represent data from flying birds; square symbols represent data from the ratites. Data for ratite humeri were not included in the calculation of the regression equation for either line. Neither slope is included in the 95% confidence interval of the other. For both regression lines $r = .99$.

would expect from structures that scale in accord with conventional engineering principles to resist static stress.

The avian wing bones in our study scale so that width is proportional to length raised to a power less than one (for the humerus, $y = 0.169x^{0.804}$; for the ulna, $y = 0.111x^{0.812}$). This means that, contrary to the direction of all other known skeletal allometries, bird wing bones become relatively thinner as they become longer (negative allometry). Because the wing bones become proportionately thinner as length increases, they should be relatively less resistant to bending stresses. The evolutionary advantages to large birds of having more limber wings are not immediately apparent, except that the increased flexibility may allow larger-winged animals to withstand greater transient stresses.

The evolution of flight has apparently required the length of the wing bones to scale at a substantially greater rate of increase, relative to increasing body mass than has that of the leg bones. These allometries are shown in figure 3. The length of the femur scales approximately to the one-third power of body mass as would be expected from the near geometric scaling which has been reported for other species (Prange 1977; Prange and Christman 1976). The length of the humerus, however, is proportional to nearly the one-half power of body mass. (The tibiotarsus and ulna share the scaling of the femur and humerus, respectively, but for clarity were not included in the figure.) By inverting the allometry it can be seen that the square of the length of the major wing bones scales almost exactly to the body mass, for example, (humerus length)$^2 \propto$ mass$^{0.964}$.

At first approximation it would appear that since wing area might be represented

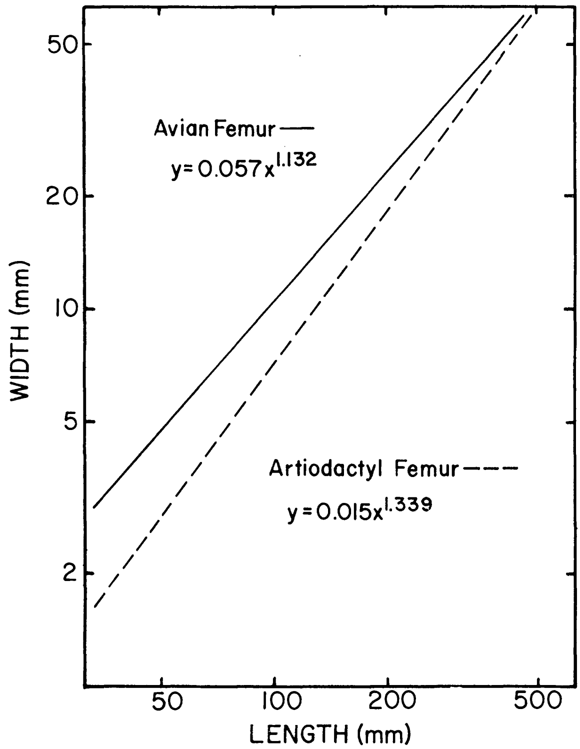

FIG. 4.—Comparison of the scaling of width (y) and length (x) of femurs of birds (this study) and artiodcatyl ungulates (McMahon 1975).

as a function of length squared and aerodynamic lift is proportional to wing area, this scaling would function to maintain a constant proportion between lift generated and the load of body weight. However, Greenewalt (1975) has shown that the width (chord) of bird wings varies allometrically with length, and hence wing area is not a simple function of length squared. Lift is also a function of airspeed and one must assume that the aerodynamic constraints on the scaling of wing dimensions require changes not only in wing area but also on factors which produce appropriate changes in airspeed. Thus the scaling of wing length may be related to the lift requirement only in the most general sense. Empirical measurement of the static and dynamic mechanical properties of the wing bones is therefore probably the most profitable course to follow to determine the function of the atypical scaling of the dimensions of avian wing bones.

The consequences of flight may also affect the leg bones of birds. Birds must support a static stress from the body weight on each leg which is probably double that of a quadruped of the same body mass. Comparison of the length to width allometry of avian femurs with those of mammals shows that, within the range of lengths common to both groups, a bird's femur of a given length is thicker than a femur of comparable length from a mammal. Figure 4 shows our data on the scaling of avian femurs together with that from the largest group from McMahon (1975), artiodactyl ungulates. At the shorter lengths the difference is more pronounced but overall the avian femurs appear to be greater in diameter for a given length. An estimate of the actual differences in strength would require more information on the mechanical properties of the bone and the scaling of wall thickness. We did not determine these properties for the specimens we measured because their value precluded destructive testing and because fresh material is required for meaningful measurements.

The explanation for the similar allometries of skeletal mass in birds and mammals may ultimately be that the structural material that is saved in the long pneumatized wing bones has had to be added to the more robust leg bones. Thus the birds may have achieved an internal redistribution of skeletal mass but not an overall relative reduction.

SUMMARY

New data on the allometric relationship of skeletal mass to body mass of birds and mammals indicate that the avian skeleton is not proportionately lighter than that of mammals. Pneumatization may make some birds bones lighter, but the leg bones of birds are more robust than those of mammals. This results in an internal redistribution rather than a reduction of skeletal mass.

ACKNOWLEDGMENTS

We are especially grateful to E. S. Wing, Associate Curator at the Florida State Museum, Gainesville, for allowing us to use her data on mammals, and P. Brodkorb and K. C. Campbell for allowing us to have access to their collections.

APPENDIX A

TABLE A1

BODY AND SKELETAL MASSES OF MAMMALS

Specimen	No. in Sample	Body Mass (kg)	Skeletal Mass (kg)	Source
Marsupialia				
Didelphidae				
Didelphis sp.	2	3.35	.193	Ziegler 1973
D. marsupialis	1	3.915	.227	Wing*
	1	2.940	.185	Wing
	1	2.650	.182	Wing
Insectivora				
Soricidae				
Sorex sp. and *Blarina* sp.	7	.0063	.0003	Ultsch 1974
Lagomorpha				
Leporidae†				
Sylvilagus palustris	1	.790	.039	Wing
	1	.820	.027	Wing

(*Continued*)

TABLE A1 (*Continued*)

Specimen	No. in Sample	Body Mass (kg)	Skeletal Mass (kg)	Source
Rodentia				
Erethizontidae				
Erethizon sp.	1	7.000	.294	Ziegler 1973
Capromyidae				
Myocastor coypus	1	4.836	.244	Wing
	1	1.920	.096	Wing
Cricetidae				
Peromyscus sp.	4	.0295	.0013	Ziegler 1973
Microtus sp.	3	.0421	.0018	Ziegler 1973
M. ochrogaster	1	.030	.002	Wing
Sciuridae				
Eutamias sp.	1	.0488	.0022	Ziegler 1973
Citellus sp.	3	.114	.0052	Ziegler 1973
Sciurus sp.	1	.845	.0417	Ziegler 1973
S. carolinensis	1	.275	.015	Wing
	1	.365	.020	Wing
Glaucomys volans	1	.030	.0025	Wing
Geomyidae				
Thomomys sp.	4	.115	.0076	Ziegler 1973
Castoridae				
Castor sp.	1	22.7	1.146	Ziegler 1973
Caviidae				
Cavia porcellus	1	.385	.0233	Wing
	1	.065	.005	Wing
Muridae†	...	...	...	...
Carnivora				
Canidae†				
Canis sp.	2	11.950	.748	Ziegler 1973
Urocyon cinereoargentatus	1	3.395	.250	Wing
	1	3.585	.197	Wing
Procyonidae				
Procyon lotor	1	3.325	.128	Wing
	1	1.390	.062	Wing
	1	3.635	.226	Wing
	1	2.460	.107	Wing
	1	4.260	.224	Wing
Procyon sp.	2	4.210	.233	Ziegler 1973
Potos sp.	1	2.250	.128	Ziegler 1973
Mustelidae				
Mustela sp.	1	.350	.0173	Ziegler 1973
Spilogale sp.	1	.149	.010	Ziegler 1973
Felidae				
Felis sp.	2	.845	.0436	Ziegler 1973
Lynx sp.	1	5.450	.323	Ziegler 1973
L. rufus	1	5.250	.295	Wing
Artiodactyla				
Cervidae				
Odocoileus virginianus	1	4.450	.270	Wing
	1	6.725	.448	Wing
	1	1.560	.135	Wing
Primates				
Hominidae†	...	...	...	...
Proboscidea				
Elephantidae†	...	...	...	...

* All references to Wing are personal communication.
† Familes are represented or have additional data in table A2.

TABLE A2

BODY AND SKELETAL MASSES OF MAMMALS

Specimen	Body Mass (kg)	Skeletal Mass (kg)	Source
Souris (mouse)	.020	.001066	Martin and Fuhrman (1955)
Rat (rat)	.205	.0129	Field, et al. (1939) Huston and Martin (1954)
Lapin (rabbit)	2.021	.181	Pfeiffer (1887)
Chat (cat)	2.931	.342	Voit (1866) Sedlmair (1899)
Chien (dog)	20.000	4.120	Martin and Fuhrman (1955) Voit (1905)
Homme (human)	67.310	12.161	Kopsch (1914)
Elephant (elephant)	6,600	1,782	Crile and Quiring (1941)

NOTE.—The data are those used by Kayser and Heusner (1964), they are given with the citations from Heusner 1963. No scientific names were used to identify specimens.

APPENDIX B

BODY AND SKELETAL MASSES OF BIRDS

Specimen	Total Body Mass (kg)	Skeletal Mass (kg)
Struthioniformes		
Struthionidae (ostriches)		
Struthio camelus	80.970	7.729
	80.920	5.792
Rheiformes		
Rheidae (rheas)		
Rhea americana	18.872	1.311
Casuariiformes		
Casuariidae (cassowaries)		
Casuarius casuarius	36.571	2.588
Dromiceiidae (emus)		
Dromiceius novae-hollandiae	40.667	1.995
Apterygiformes		
Apterygidae (kiwis)		
Apteryx australis mantelli	2.170	.156
Tinamiformes		
Tinamidae (tinamous)		
Rhynchotus rufescens	.766	.034
Crypturellus soui panamensis	.237	.010
C. cinnamomeus praepus	.371	.016
Sphenisciformes		
Spheniscidae (penguins)		
Spheniscus humboldti	3.914	.244
Procellariiformes		
Diomedeidae (albatrosses, etc.)		
Diomedea epomorphora sandfori	7.500	.665
Procellariidae (shearwaters)		
Puffinus griseus	.801	.037

(*Continued*)

APPENDIX B (*Continued*)

Specimen	Total Body Mass (kg)	Skeletal Mass (kg)
Podicipediformes		
Podicipedidae (grebes)		
Podiceps major	1.202	.055
	1.108	.069
	1.225	.072
	1.158	.067
	1.206	.073
	1.136	.062
Poliocephalus ruficollis	.163	.0054
Gaviiformes		
Gaviidae (loons)		
Gavia immer elasson	2.150	.253
G. stellata	1.351	.084
Pelecaniformes		
Phaethontidae (tropic birds)		
Phaethon lepturus catesbyi	.395	.020
Pelecanidae (pelicans)		
Pelecanus occidentalis	3.330	.270
	2.504	.203
Sulidae (boobies)		
Sula nebouxii	1.220	.085
Phalacrocoracidae (cormorants)		
Phalacrocorax africanus	.522	.036
	.526	.031
P. carbo	1.582	.100
Anhingidae (anhingas)		
Anhinga anhinga leucogaster	1.028	.082
A. rufa	1.224	.095
Ciconiiformes		
Ardeidae (heronlike birds)		
Ardea goliath	3.285	.405
A. purpurea	.886	.062
A. h. herodias	1.680	.096
Butorides striatus	.290	.012
Casmerodius albus	.877	.075
Egretta garzetta	.453	.032
E. thula	.361	.027
Scopidae (hammerheads)		
Scopus umbretta	.355	.027
Ciconiidae (storks)		
Anastomus lamelligerus	1.047	.082
	1.419	.120
Sphenorhynchus abdimii	1.008	.068
Ibis ibis	2.696	.269
Phoenicopteridae (flamingos)		
Phoeniconaias minor	1.523	.108
Anseriformes		
Anatidae (ducks and geese)		
Aythya erythrophthalma	.861	.041
	.821	.038
	.701	.043
Oxyura jamaicensis rubida	.416	.027
Cygnus buccinator	10.773	.824

(*Continued*)

APPENDIX B (*Continued*)

Specimen	Total Body Mass (kg)	Skeletal Mass (kg)
Falconiformes		
Sagittariidae (secretary bird)		
Sagittarius serpentarius	3.813	.301
	3.409	.255
Accipitridae (Old World vultures, hawks, and eagles)		
Buteo jamaicensis umbrinus	.962	.073
	1.244	.090
B. lineatus alleni	.592	.040
Heterospizias meridionalis	.763	.060
Necrosyrtes monachus	1.882	.143
	1.525	.143
Neophron percnopterus	2.134	.138
Haliaeetus leucocephalus	4.082	.272
Falconidae (falcons and caracaras)		
Aquila rapax	1.954	.146
	2.379	.186
Butastur rufipennis	.305	.027
Circus macrourus	.416	.025
C. pygargus	.286	.022
Falco naumanni	.124	.0058
F. rupicoloides	.207	.013
	.180	.012
F. sparverius	.100	.00682
	.103	.00621
	.082	.00493
	.117	.0069
	.091	.00536
	.091	.00590
F. tinnunculus	.208	.013
	.191	.014
Melierax gabar	.168	.011
	.124	.00784
Melierax poliopterus	.561	.047
	.514	.051
Milvus migrans	.567	.046
Poliohierax semitorquatus	.057	.00406
Polyborus plancus	1.072	.088
Galliformes		
Phasianidae (pheasants, quails, and partridges)		
Acryllium vulturinum	1.607	.088
	1.641	.085
Francolinus sephaena	.263	.012
Numida meleagris	1.281	.067
Pternistis leucoscepus	.576	.028
	.644	.027
Meleagrididae (turkeys)		
Meleagris gallopavo osceola	2.453	.317
Gruiformes		
Gruidae (cranes)		
Grus canadensis tabida	4.280	.283
	4.990	.297
	5.443	.351
G. canadensis pratensis	2.360	.214

(*Continued*)

APPENDIX B (*Continued*)

Specimen	Total Body Mass (kg)	Skeletal Mass (kg)
Gruiformes (*Continued*)		
Rallidae (rail-like birds)		
Fulica cristata	.686	.036
Porphyrio alba	.598	.040
	.672	.048
	.427	.028
	.632	.044
Rallus longirostus	.306	.0123
Otididae (bustards)		
Choriotis kori	6.300	.388
Neotis heuglinii	2.830	.135
Charadriiformes		
Jacanidae (jacanas)		
Actophilornis africanus	.156	.0129
	.132	.0116
	.189	.015
Haematopodidae (oystercatchers)		
Haematopus palliatus	.615	.033
Charadriidae (plovers)		
Charadrius asiaticus	.071	.0036
C. pecuarius	.030	.00181
	.030	.00188
	.023	.00138
	.031	.00174
	.032	.00171
	.029	.00182
C. tricollaris	.028	.00176
	.029	.00165
Hoplopterus spinosus	.150	.011
Squatarola squatarola	.191	.00844
Stephanibyx coronatus	.127	.011
	.148	.011
	.171	.011
	.170	.011
	.156	.011
Scolopacidae (sandpipers and their allies)		
Calidris minuta	.018	.00112
	.024	.00098
	.019	.00113
Calidris temminckii	.020	.00102
Calidris testacea	.055	.00267
Ereunetes mauri	.025	.00105
	.024	.00106
Catoptrophorus s. semipalmatus	.0255	.0013
Crocethia alba	.049	.00236
Limosa limosa	.214	.014
Totanus melanoleucus	.214	.0105
Tringa glareola	.047	.00259
	.056	.00306
	.051	.00279
Tringa hypoleucos	.045	.00217
Tringa ocrophus	.076	.00371

(*Continued*)

APPENDIX B (*Continued*)

Specimen	Total Body Mass (kg)	Skeletal Mass (kg)
Charadriiformes (*Continued*)		
Recurvirostridae (stilts and avocets)		
Recurvirostra avosetta	.247	.019
Burhinidae (thick-knees)		
Burhinus senegalensis	.306	.021
	.330	.023
B. superciliaris	.446	.035
	.452	.029
Glareolidae (pratincoles and coursers)		
Glareola pratincola	.071	.00366
	.062	.00405
	.062	.00361
	.068	.00424
Laridae (gulls and terns)		
Chlidonias leucoptera	.073	.00427
	.052	.00367
	.061	.00334
C. nigra surinamensis	.056	.00243
Gelochelidon nilotica	.206	.014
	.211	.013
Hydroprogne caspia	.690	.048
Larus dominicanus	1.243	.080
	1.242	.079
	1.053	.078
	1.298	.070
L. cirrocephalus	.345	.024
	.383	.024
	.302	.018
	.368	.023
Sterna albifrons antillarum	.045	.00258
	.047	.00254
	.046	.00230
	.047	.00249
Columbiformes		
Pteroclidae (sandgrouse)		
Pterocles exustus	.183	.00866
	.209	.00951
Columbidae (pigeons and doves)		
Columbigallina p. passerina	.031	.00102
	.048	.00129
Oena capensis	.031	.00082
Streptopelia capicola	.113	.00490
S. decipiens	.144	.00618
	.135	.00616
S. senegalensis	.090	.00370
Zenaida asiatica	.196	.00779
	.211	.00969
Zenaida auriculata	.132	.00369
	.129	.00427
	.124	.00380
Zenaidura macroura	.106	.00407

(*Continued*)

APPENDIX B (*Continued*)

Specimen	Total Body Mass (kg)	Skeletal Mass (kg)
Psittaciformes		
Psittacidae (parrots and their allies)		
Agapornis fischeri	.035	.00245
	.038	.00184
Agapornis personata	.037	.00267
Aratinga erythrogenys	.200	.0095
Forpus coelestes	.032	.00148
	.029	.00141
	.027	.00123
	.027	.00116
Pionus chalcopterus	.254	.0102
Poicephalus rufiventris	.132	.0105
Psittacus erithracus	.290	.017
	.296	.024
Cuculiformes		
Musophagidae (tauracos)		
Crinifer leucogaster	.231	.011
Tauraco hartlaubi	.269	.012
	.257	.011
Cuculidae (cuckoos, roadrunners, and anis)		
Centropus superciliosus	.132	.0064
Strigiformes		
Strigidae (owls)		
Ciccaba nigrolineata	.430	.036
Glaucidium brasilianum	.061	.00384
G. perlatum	.0069	.00467
Speotyto cunicularia floridana	.182	.00796
	.179	.00742
	.185	.00754
Caprimulgiformes		
Caprimulgidae (night jars)		
Caprimulgus europaeus	.048	.00303
	.047	.00282
Chordeiles minor	.069	.00297
Scotornis climacurus	.035	.00149
Apodiformes		
Apodidae (swifts)		
Apus affinis	.026	.00137
Trochilidae (hummingbirds)		
Phaethornis superciliosus	.00360	.00025
Archilochus colubris	.0035	.000088
Coliiformes		
Coliidae (mousebirds)		
Colius macrourus	.045	.00183
	.051	.00243
	.054	.00343
Trogoniformes		
Trogonidae (trogons)		
Trogon personatus	.053	.00196
T. violaceus	.052	.00177

(*Continued*)

APPENDIX B (*Continued*)

Specimen	Total Body Mass (kg)	Skeletal Mass (kg)
Coraciiformes		
Alcedinidae (kingfishers)		
Ceryle rudis	.058	.00418
Corythornis cristata	.013	.00091
Halcyon leucocephala	.042	.00257
Megaceryle a. alcyon	.156	.0071
Meropidae (bee-eaters)		
Melittophagus revoilii	.015	.00085
	.014	.00080
	.015	.00084
	.013	.00078
	.013	.00076
	.015	.00082
Merops nubicus	.046	.00276
Merops superciliosus	.047	.00235
Coraciidae (rollers)		
Coracias garrulus	.103	.00691
C. naevia	.151	.0102
Phoeniculidae (woodhoopoes)		
Phoeniculus purpureus	.090	.00655
Rhinopomastus minor	.022	.00125
Bucerotidae (hornbills)		
Aceros undulatus	1.431	.142
Tockus deckeni	.169	.01075
T. erythrorhynchus	.130	.010
T. flavirostris	.201	.014
Piciformes		
Capitonidae (barbets)		
Trachyphonus erythrocephalus	.060	.00423
Tricholaema melanocephalum	.020	.00120
	.021	.00129
	.023	.00128
Picidae (woodpeckers)		
Campethera nubica	.057	.00346
	.055	.00330
Dendrocopus villosus	.059	.00322
D. pubescens	.025	.00108
Melanerpes pucherani	.058	.00277
Picumnus olivaceus	.0087	.00049
Veniliornis callonotus	.029	.00160
Passeriformes		
Dendrocolaptidae (woodcreepers)		
Dendrocincla tyrannina	.031	.00163
Furnariidae (ovenbirds)		
Furnarius leucopus	.041	.00251
Geositta peruviana	.020	.00082
	.016	.00058
Synallaxis brachyura	.0126	.00062
Formicariidae (antbirds)		
Gymnopithys leucaspis	.030	.00130
Sakesphorus bernardi	.032	.00141
	.029	.00145

(*Continued*)

APPENDIX B (*Continued*)

Specimen	Total Body Mass (kg)	Skeletal Mass (kg)
Passeriformes (*Continued*)		
Pipridae (manakins)		
Manacus manacus	.0137	.00061
	.017	.00062
Tyrannidae (tyrant flycatchers)		
Camptostoma obsoletum	.007	.00026
Contopus cinereus	.0094	.00039
	.0105	.00044
Elaenia flavogaster	.021	.00097
Empidonax virescens	.013	.00054
Euscarthmus meloryphus	.0045	.00021
Myiobius barbatus	.0078	.00031
Pipromorpha oleaginea	.0104	.00049
Todirostrum cinereum	.0053	.00021
Tyrannus tyrannus	.043	.00164
Tyrannus d. domincensis	.042	.00181
Hirundinidae (swallows)		
Hirundo aethiopica	.013	.00067
Ptyonoprogne fuligula	.016	.00078
	.015	.00077
Corvidae (crows, jays, and magpies)		
Corvus corax	.457	.034
Corvus ossifragus	.209	.014
Cyanocorax mystacalis	.148	.00751
Aphelocoma c. coerulescens	.0731	.0036
Paridae (titmice)		
Parus carolinensis	.0077	.00024
Sittidae (nuthatches)		
Sitta pusilla	.0097	.00039
Troglodytidae (wrens)		
Campylorhynchus fasciatus	.037	.00168
Thryothorus maculipectus	.0122	.00062
Sylviidae (Old World warblers)		
Polioptila plumbea	.0035	.00020
	.0035	.00021
	.0063	.00021
Ramphocaenus melanurus	.0078	.00037
Bombycillidae (waxwings)		
Bombycilla cedrorum	.036	.00128
	.033	.00129
Lanriidae (shrikes)		
Lanius l. ludovicianus	.050	.00161
Vireonidae (vireos)		
Vireo olivaceus	.0118	.00061
	.0131	.00064
Coerebidae (honeycreeper)		
Coereba flaveola	.0083	.00039
Parulidae (woodwarblers and bananaquits)		
Dendroica petechia	.0088	.00052
D. pinus florida	.014	.00058
Helmitheros vernivorus	.013	.00061
Parula a. americana	.0073	.00031
Oporornis philadelphia	.0136	.00037

(*Continued*)

APPENDIX B (*Continued*)

Specimen	Total Body Mass (kg)	Skeletal Mass (kg)
Passeriformes (*Continued*)		
Icteridae (tropicals)		
Agelaius phoeniceus floridanus	.0318	.00134
Emberizidae (= Fringillidae in part: seedeaters)		
Ammospiza maritima peninsulae	.021	.00090
Arremon abeillei	.022	.00118
Arremonops conirostris	.038	.0191
Atlapetes brunneinucha	.036	.00202
Cyanocompsa cyanoides	.026	.00145
Oryzoborus angolensis	.0092	.00061
	.0099	.00058
	.0112	.00070
Pipilo e. erythrophthalmus	.040	.00172
Pooecetes g. gramineus	.027	.00119
Rhodospingus cruentus	.0094	.00047
Saltator maximus	.050	.00241
Sicalis flaveola	.019	.00117
Spizella p. passerina	.013	.00051
Sporophila peruviana	.0088	.00052
Volatinia jacarina	.0082	.00037
Zontrichia albicollis	.032	.0011

NOTE.—The taxonomic organization of the bird data follows that of Wetmore (1960).

APPENDIX C

Avian Skeletal Dimensions

Specimen	Body Mass	Skeletal Mass	Femur	Tibio-tarsus	Humerus	Ulna
Phaethornis superciliosus	.0036	.00025	8.38/0.58	...	5.10/1.12	...
			8.37/0.53	...	...	...
Todirostrum cinereum	.0053	.00021	10.20/0.87	19.95/0.77	10.25/1.02	...
			...	19.80/0.74	10.12/1.01	...
Parus carolinensis	.0077	.00024	10.26/0.94	18.83/1.02	11.96/1.18	...
			10.34/0.96	18.87/0.96	...	...
Empidonax virescens	.013	.00054	13.24/0.97	21.94/0.96	14.74/1.53	21.20/1.20
			13.27/1.00	22.21/0.95	...	21.11/1.26
Bombycilla cedrorum	.036	.00128	18.1/1.3	28.8/1.2	20.5/2.0	24.7/1.6
			18.0/1.3	28.8/1.2	20.1/2.0	24.4/1.6
Dendrocopus pubescens	.025	.00108	14.6/1.4	22.2/1.2	20.8/1.6	23.2/1.4
			14.6/1.4	...	20.6/1.6	23.2/1.4
Chordeiles minor	.069	.00297	20.7/1.5	28.7/1.4	38.6/3.0	46.2/2.6
			20.9/1.6	28.8/1.5	38.9/3.0	...
Coracias garrulus	.103	.00691	26.8/2.6	39.8/2.2	51.2/3.3	59.1/2.9
			27.1/2.6	...	51.1/3.2	58.9/2.9
Squatarola squatarola	.191	.00844	34.9/2.6	68.1/2.5	51.5/3.4	54.3/3.3
			...	67.6/2.5	51.9/3.5	54.4/3.3
Phalacrocorax africanus	.522	.036	38.5/4.9	64.3/3.2	99.7/4.3	99.2/3.7
			38.6/4.9	64.3/3.1	100.1/4.3	98.3/3.7
Ardea purpurea	.886	.062	81.7/5.9	170/5.7	135.1/6.6	151/4.9
			81.7/5.9	171/5.7	134.8/6.4	...
Buteo jamaicensis	.962	.073	82.7/8.5	113/7.7	113/8.4	128/6.7
			82.9/8.6	112/7.9	...	128/6.6
Ibis ibis	2.096	.269	96/10.3	272/8.4	180/9.9	217/7.4
			96/10.4	269/8.7	181/10.2	216/7.3
Pelecanus occidentalis	2.504	.203	75.7/9.3	111.5/7.6	254/11.6	300/10.0
			76.6/9.2	111.7/7.7	...	302/10.3
Sagittarius serpentarius	3.409	.255	97.1/11.7	...	174/12.4	178/8.9
			...	...	...	...
Choriotus kori	6.300	.388	110/14.5	247/13.2	212/16.9	246/10.9
			109/14.5	247/13.2	213/16.4	246/10.5

Cygnus buccinator	10.773	.824	119/11.6	211/12.4	303/18.8	296/13.6
			119/11.6	212/12.5	303/18.7	295/13.1
Rhea americana	18.872	1.311	190/22.3	322/24.3	264/12.0	187/4.8
			190/22.5	321/23.9	266/11.9	188/4.8
Casuarius casuarius	36.571	2.588	205/27.6	361/26.1	98.5/8.4	67.1/5.2
			203/27.4	356/26.3	98.9/8.2	...
Dromecius novae-hollandiae	40.667	1.995	187/27.8	342/26.0	...	...
			187/27.2	345/25.7	...	...
Struthio camelus	80.920	5.792	286/46.1	534/36.2	367/14.3	...
			284/46.4	535/36.7	369/15.3	...
Struthio camelus	80.920	7.792	295/54.4	575/46.1	382/17.5	...
			294/54.9	574/41.1	380/16.6	...

NOTE.—Dimensions are given as length/thickness in millimeters. Cases where a given bone was broken and could not be measured, showed evidence of a healed fracture, or could not be identified with certainty are indicated by an ellipsis (···). Body and skeletal masses are given in kilograms.

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