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Source: *The American Naturalist*, Vol. 113, No. 1 (Jan., 1979), pp. 103-122
Published by: The University of Chicago Press for The American Society of Naturalists
Stable URL: http://www.jstor.org/stable/2459945
Accessed: 18/04/2013 13:27

# 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

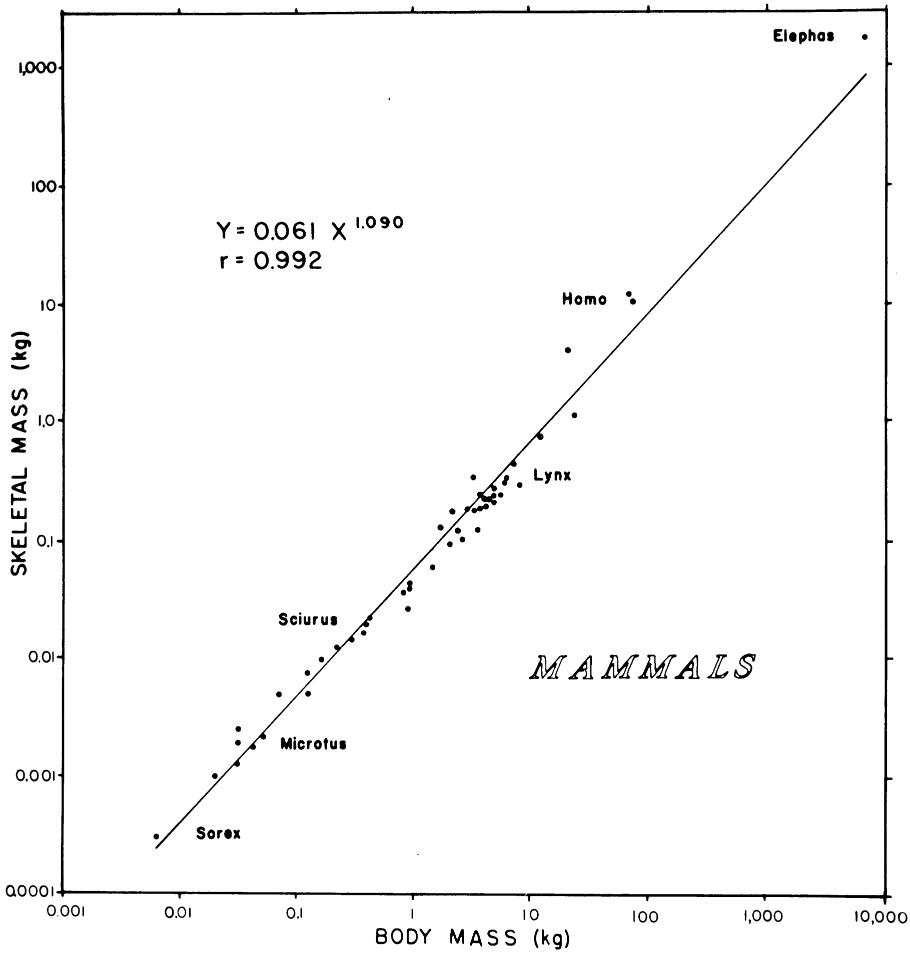


FIG. 1.—Relationship between skeletal mass ($y$) and body mass ($x$) for mammals. The sample for the logarithmic regression consisted of 49 data; the standard error of estimate for $y$ on $x$ was 0.154; the range of body mass values included in the sample was 0.006–6,600 kg. Examples of representative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

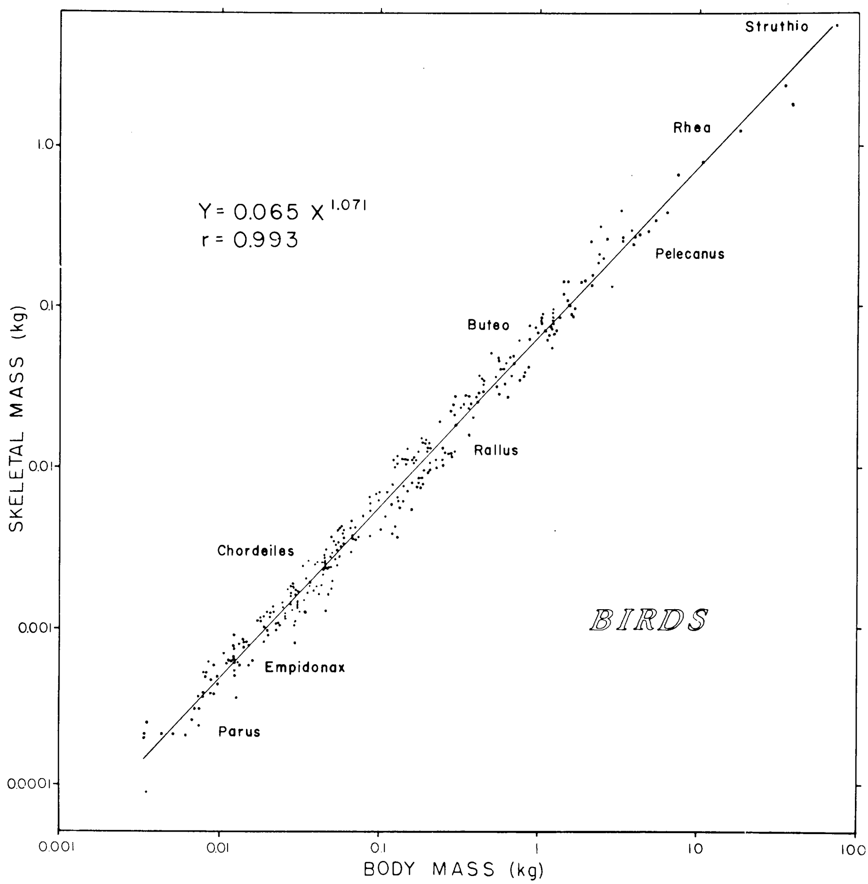


FIG. 2.—Relationship between skeletal mass ($y$) and body mass ($x$) for birds. The sample for the logarithmic regression consisted of 311 data; the standard error of estimate for $y$ on $x$ was 0.102; the range of body mass values included in the sample was 0.0031–80.920 kg. Examples of representative 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

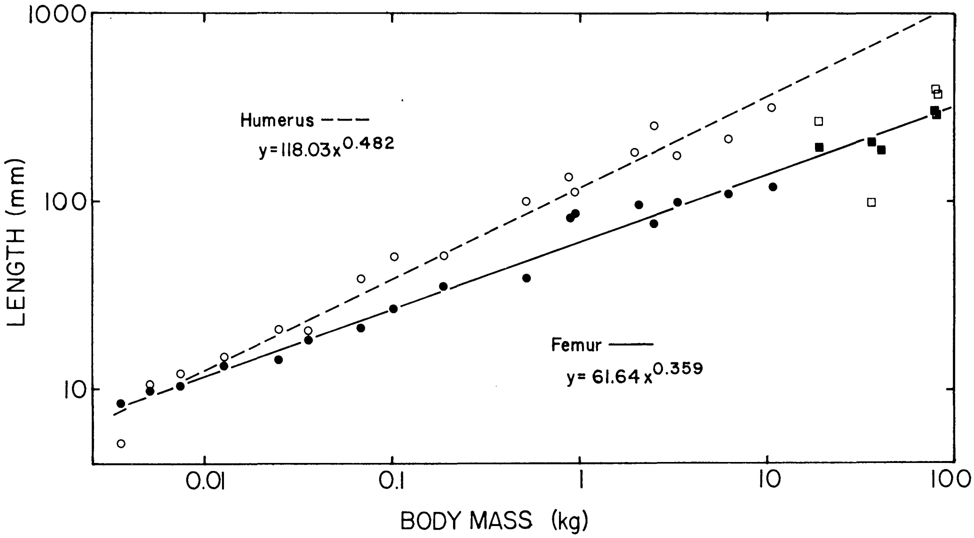


FIG. 3.—Relationship between the length ($y$) of avian femur and humerus and body mass ($x$). Open symbols (○, □) refer to the humerus; solid symbols (●, ■) refer to the femur; circular symbols represent data from flying birds; square symbols represent data from the ratites. Data for ratite humeri were 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, $(\text{humerus length})^2 \propto \text{mass}^{0.964}$.

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

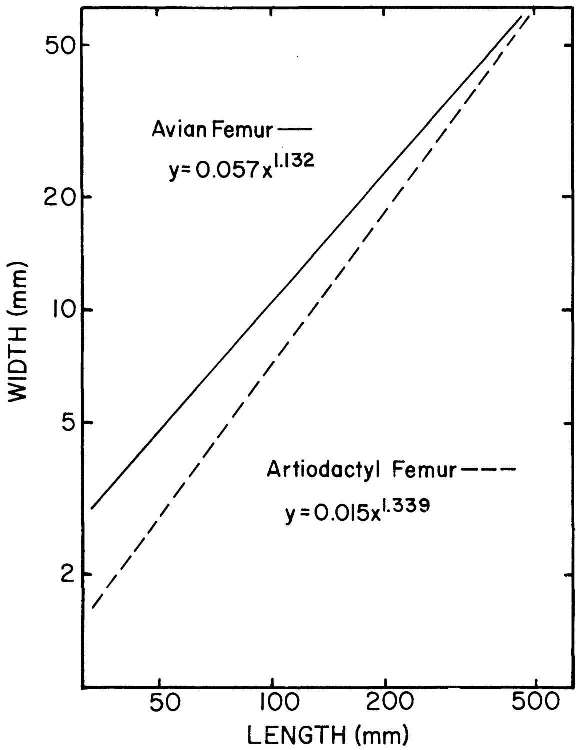


FIG. 4.—Comparison of the scaling of width ($y$) and length ($x$) of femurs of birds (this study) and artiodcatyl ungulates (McMahon 1975).

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)<br>Huston and Martin (1954) |
| Lapin (rabbit) | 2.021 | .181 | Pfeiffer (1887) |
| Chat (cat) | 2.931 | .342 | Voit (1866)<br>Sedlmair (1899) |
| Chien (dog) | 20.000 | 4.120 | Martin and Fuhrman (1955)<br>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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