AN ESTIMATED WEIGHT OF THE LARGEST KNOWN BIRD

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The Ostrich (*Struthio camelus*), largest of living birds, was far surpassed in size by the Elephant-bird (*Aepyornis maximus*) of Madagascar. The larger of the New Zealand moas such as *Dinornis* were intermediate in size. The moas and elephant-birds were exterminated by the natives of these islands and are known only from sub-fossil remains of skeletons, eggs and feathers. An estimate of the weight of the largest known birds may be of both scientific and popular interest. Although the living ratites may not be closely related to the extinct ones of Madagascar and New Zealand, they are the closest approach to them in size and proportions, and may be used as a basis for calculations. This study was undertaken at the suggestion of Dr. Ernst Mayr, and he has given me a number of valuable suggestions.

MATERIALS AND MEASUREMENTS

The species used in this study are as follows:

Aepyornithidae. Elephant-birds: *Aepyornis maximus, Mullerornis agilis.*

Dinornithidae. Moas: *Dinornis maximus, D. giganteus, Euryapteryx* sp.

The two species of *Dinornis* were probably geographical representatives on the two principal islands of New Zealand. The skeleton of *Euryapteryx* which was examined, according to Oliver's (1930) key, would represent *E. pygmaeus.*

Apterygidae. Kiwis: *Apteryx* sp.

Casuariidae. Cassowaries: Measurements of the small species, *C. bennetti,* were not used. Most of the measurements available for the larger cassowaries (*C. casuarius* and *C. unappendiculatus*) were not identified to species and were combined.

Dromaeidae. Emus: *Dromaeus n. hollandiae.*

Rheidae. Rheas: *Rhea americana.*

Struthionidae. Ostrich: *Struthio camelus.*

The Casuariidae and Dromaeidae belong to the same order. The Apterygidae are related to the Dinornithidae, though less closely. Except for these, the families listed above are believed to be no more closely related to each other than to various orders of flying (carinate) birds.

Measurements used are as follows:

Body length, measured from the anterior border of the thorax to the center of the acetabulum. Although this measurement falls on a diagonal, it seemed most satisfactory of several tried while seeking an over-all measure of general body size. In *Aepyornis* and *Mullerornis* this measurement was estimated from photographs of articulated skeletons published by Monnier (1913) and Lamberton (1934), respectively, by taking a ratio between body length and a known measurement such as the tibiotarsus.

Femur area, the area of the cross section of the femur calculated from its circumference measured at its smallest point near the center of the shaft.

Egg weight, the approximate weight in kilograms. In a previous paper (Amadon, 1943*a*) I have summarized earlier formulas which show that the volume of an egg in cubic centimeters is roughly equal to one-half its length times its breadth squared ($0.5\ LB^2$), measurements being to the nearest centimeter. This calculation also corresponds approximately to the weight of the egg in grams, since the specific gravity of a fresh egg is about 1. As interest for present purposes is in relative rather than absolute egg weights, use of this formula is satisfactory. Real errors in relative egg weights result from differences in egg shape (for example, the egg of the Ostrich is rounder than those of other living ratites), but it would be difficult to work out a compensation for this error.

Limb bones, the over-all length of the bones. The flaring process at the proximal end of the tibiotarsus, which is especially large in the Emu, was not included in the measurement.

Weights of ratites are given by Stresemann (1927-1934), Heinroth (1922) and, for the Ostrich only, by Newton (1893-1896). Most of these weights were based on a small but unstated number of captive specimens, usually of uncertain sex, age and sometimes specific identity. Stresemann's weight for the Emu, which exceeds that of the Ostrich, was considered an error and was not used. Mr. Karl Plath of the Chicago Zoo kindly advises me that the Ostrich weighs about 300 pounds, while Mr. Malcolm Davis states that the weight of a large example of *Casuarius unappendiculatus occipitalis* that died in the Washington Zoo was 115 pounds. The margin of error in a study like the present would be much reduced if the weights of the individual birds whose skeletons were measured were known, but in no instance was this true.

The egg measurements of living ratites are from specimens in the American Museum except for the Ostrich, for which a series measured by Rothschild (1918-1919) was used. For *Aepyornis* measurements of a series supplied by Lambrecht (1933) were combined with those of one specimen in the American Museum. Only five eggs of moas are known. The largest of these is considered by Oliver (1930) to represent *Dinornis maximus*. Oliver's measurements of this egg were used.

Measurements of the skeletons of living ratites and of *Euryapteryx* are from specimens in the American Museum of Natural History. The body length measurement in particular is based on only one or two specimens for each species. Measurements of *Aepyornis* are from Monnier (1913), of *Mullerornis* from Lamberton (1934), and of *Dinornis* from Oliver (1930) and Owen (1879). The actual measurements used are given in table 1. Weights are in kilograms, areas in square centimeters and length in centimeters. The body lengths given beyond are not included.

Table 1

Measurements of Skeletons of Ratites

	Body Weight	Egg Weight	Femur area	Femur length	Tibiotarsus length	Tarsometatarsus length
Aepyornis maximus	....	7.762	60	44	77	45
Mullerornis agilis	....	....	12.6	25.7	44.5	31.8
Dinornis maximus	....	4.008	33	43	92	50
Euryapteryx	....	....	15.6	23	37	15
Apteryx (Kiwi)	2.5	.371	......	10	13.5	7
Struthio camelus (Ostrich)	100	1.314	15.6	39	53	49
Dromaeus n. hollandiae (Emu)	47	.535	8.0	22.6	40.1	39.5
Casuarius (Cassowary)	42.5	.633	6.1	22.3	38.5	32.5
Rhea americana (Rhea)	20	.563	5.1	21.5	33.5	32

If measurements correlated with weight are known for the living ratites and the same measurements are available for the extinct species, the weight of the latter can be estimated by proportion. A ratio diagram (fig. 27) was made to determine which species and which measurements are most suitable for such comparisons. This type of logarithmic ratio diagram was devised by Simpson (1941). He gives a complete explanation which is summarized and, in part, quoted here.

A logarithmic graphing of ratios has two advantages: (1) On a logarithmic graph equal relative variation is represented by equal distance. For example, the difference between the logarithms of 10 and 100 is the same as that between those of 100 and 1000 and the ratios of these two pairs of numbers is the same. In figure 27 the Ostrich is taken as the standard of comparison (ratio 1.00). The ratio of a given measurement of any of the other species to the corresponding measurement for the Ostrich may be read directly from the ratio scale at the bottom of the graph. "Although the differences are thus calculated from some one standard, the resulting diagram shows not only ratios to that standard but ratios of any combinations of observations. . . . By copying this scale on a separate slip of paper, a movable scale can be made and the diagrams have the property that if 1.00 on the ratio scale be set at any specimen (whether the standard or not), the values of the ratios of all other specimens (set on the same horizontal) to

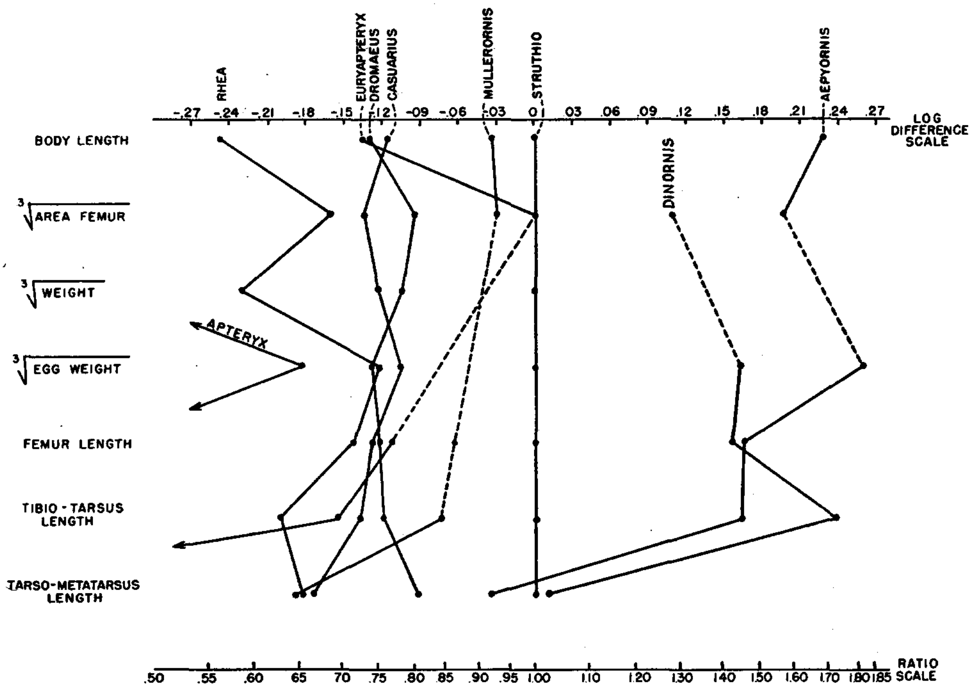

Fig. 27. Comparison by ratio diagram of selected measurements of certain ratites (see text).

this one can at once be read on the scale." (2) Logarithmic ratio diagrams are easily constructed without computing any of the numerous ratios represented thereon. The difference between the logarithms of two numbers corresponds to the ratio of the numbers (division is performed by subtracting logarithms). Since plotting logarithms on arithmetic graph paper is equivalent to plotting antilogarithms (arithmetic numbers) on logarithmic paper, the logarithms of the ratios are plotted directly on arithmetic paper. Figure 27 was plotted on millimeter graph paper with a scale of .03 difference in logarithms equal to 10 millimeters. The only arithmetic used in plotting the first line of entries of figure 27 is as follows: the computed figures shown in table 2 and along the top line of figure 27. The logarithms of the ratios of the other characters measured were computed in the same way.

Table 2

Comparison of Body Lengths in Ratites

Species	Measurement	Logarithm	Difference from logarithm of standard of comparison
Aepyornis maximus	92.7 cm.	1.96708	+ .22672
Mullerornis agilis	51	1.70757	— .03279
Dinornis maximus	(measurement not available)		
Euryapteryx (? *pygmaeus*)	40	1.60206	— .13830
Struthio camelus	55	1.74036	0 (is standard)
Dromaeus n. hollandiae	40.5	1.60746	— .13290
Casuarius	42	1.62325	— .11711
Rhea americana	31	1.49136	— .24900

In general, few measurements were available and the conclusions based upon them are only approximate. For egg weights and body weights the cube root was used to make them proportional to the linear measurements. The cross sectional area of certain bones which must support an animal's weight, such as the femur or the centra of the vertebrae, tends to be proportional to its weight (for references see Amadon, 1943*b*). In figure 27 the cross-section area of the femur is such a measurement; its cube root (the logarithm divided by 3) was used to make it directly comparable with the similarly represented body weights.

In such ratio diagrams the species or specimen selected as the standard of comparison will be represented by a straight vertical line; other species with the same proportions by lines parallel to it; while differences in proportion will be relative to the divergence from such parallel lines. Considering first the three variates of body length, area of femur and body weight, it will be seen from figure 27 that, except for the Rhea and *Euryapteryx,* these measurements, where available, are roughly proportional to the same measurements for the Ostrich. The body length of the Emu is slightly shorter than in the Cassowary but for this measurement of the Emu, only one small articulated skeleton and one partially articulated skeleton were available. Better material would probably show the Emu to average larger than the Cassowary in this measurement, as in most others. The Rhea also was represented by poor material. Its femur seems to be relatively greater in cross-sectional area as compared with body length and weight than in the other living ratites but this requires confirmation. In the small moa, *Euryapteryx,* on the other hand, the legs are undoubtedly massive out of proportion to body size or weight. The area of its femur equals that of the Ostrich, though *Euryapteryx* was a much smaller bird.

The relative egg weight of *Aepyornis* and *Dinornis* was about the same or only slightly greater than in the larger of the living ratites. The expected decrease in relative egg weight with increase in body size (Amadon 1943*a*) is not found. This need occasion no surprise since the groups here compared are only distantly related. As shown below, the weight of *Aepyornis* was probably about twice that of *Dinornis*. The eggs of the two species are not out of proportion to their body weights as some authors, misled by the very long legs of *Dinornis,* have assumed. Edinger (1943), for example, sought to explain the supposedly disproportionately large eggs of *Aepyornis* as a result of the hyperpituitarism characteristic of many giant animals (since domestic fowls fed pituitary extract laid larger eggs than before). Edinger did not mention the Kiwi (*Ayteryx*), a pygmy among the ratites, which weighs only about 2.5 kilograms but lays a huge egg of about 0.317 kilograms, the largest relative to the weight of the bird in the entire class Aves. The Rhea also lays a relatively large egg but does not rival the Kiwi. That of the Emu is rather small.

As would be expected the leg bones vary in length independently of weight or of measurements correlated with weight. Most noticeable is the great relative shortening of the tarsometatarsus in the four fossil species. Gregory (1912) found that in cursorial ungulates such as antelopes, the femur and humerus are relatively short and the distal limb segments relatively long; in ponderous species such as elephants or titanotheres the opposite is true. The relatively short tarsometatarsi of moas and elephant-birds may be correlated with their increased bulk, for these birds correspond to the ponderous or "graviportal" type of mammal. Yet the small moa, *Euryapteryx,* also has a relatively very short and heavy tarsus, suggesting that such proportions were correlated with absence of predation and sluggish locomotion rather than merely with weight as such.

ESTIMATE OF WEIGHTS

Of the measurements discussed above, the body length and the area of the femur are the only ones which, on the basis of the diagram and other considerations, seem to be correlated with weight. The proportions of the Cassowary appear most like those of

Aepyornis, so this species was used in estimating the weights of *Aepyornis* and *Dinornis*. The results are much the same if the Emu or Ostrich is used.

Using the proportion of body length : cube root of weight, the weight of *Aepyornis* may be estimated as follows:

$$\frac{\text{Body length Cassowary (42)}}{\text{Body length } \textit{Aepyornis} \text{ (92.7)}} = \frac{\text{Cube root weight Cassowary (3.49)}}{\text{Cube root weight } \textit{Aepyornis} \text{ (x)}}$$

Solution of this equation gives 457 kilograms as the estimated weight of *Aepyornis*. Using another proportion, femur area : weight, gives an estimate of 418 kilograms. The average of these two is 438 kilograms or about 965 pounds. This estimate is based on average measurements of *Aepyornis*.

The weight of *Dinornis maximus* estimated from the proportion of femur area : weight was 230 kilograms. To give another estimate, the weight of *Dinornis giganteus*, a species of about the same size or slightly smaller, was estimated from plate 30 of Owen (1879, vol. 2) in which body outlines of *D. giganteus* and *Casuarius casuarius* are represented to scale. The following ratios were taken from this figure: 1, a diagonal from the upper front border of the pelvis to the posterior border of the acetabulum; 2, the total length of the pelvis; 3, the distance from the front border of the thorax to the posterior border of the pelvis as measured in a straight line passing just above the acetabulum. The average of these ratios for the two species is 56:100. Forming from this a proportion based on the cube root of the weight gives an estimated weight for *D. giganteus* of 242 kilograms.

SUMMARY

Based on comparison with living ratites, the weight of the largest known bird, *Aepyornis maximus* of Madagascar, is estimated at 438 kilograms or 965 pounds and the weight of the largest moas (genus *Dinornis*) as about 236 kilograms or 520 pounds. This compares with a weight of about 100 kilograms or 220 pounds in the largest living bird, the Ostrich, although the latter may reach at least 300 pounds. The proportions and the size of the egg in various ratites are considered.

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